The Ecology of Lowland Totara in South Island, New Zealand

Distribution, Regeneration, and Future Survival in a Fragmented Landscape

R.L.Ebbett

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School of Forestry
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Plate 1 Large *Podocarpus totara* in matai-dominated Price's Valley Covenant, Banks Peninsula.

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ABSTRACT

Historically, lowland totara was a common forest tree throughout much of lowland New Zealand but is now confined to small, mainly protected, areas usually as the dominant species in mixed podocarp forest with matai and kahikatea. Lowland podocarp forest has suffered the most extensive reduction of all New Zealand forest types, with only circa 1% of the original forest cover remaining. The lowland totara dominated stands remaining therefore represent an highly fragmented population with relatively few individuals, making the collection of large data sets difficult. Sample sizes are small in some stands due to the limited area of totara dominated forest (circa 1 hectare).

The present study aims to describe the natural extent of lowland totara forest, document its reduction and current status, and to provide for the long-term survival of this species in the now fragmented forest environment.

Literature relating to the ecology of *Podocarpus totara* is reviewed with respect to vegetative morphology and growth, reproductive biology, timber properties and utilisation, and population dynamics. The ecological niche of lowland totara is defined, examining site characteristics and soil type. The distribution of lowland totara dominated stands is a function of several interlinked site characteristics such as climate, landform, drainage, disturbance regime, soil type, and altitude. Lowland totara appears to be confined to semi-fertile or fertile soils which are the result of landform and disturbance e.g. flood events on a river plain.

Stand descriptions identify lowland totara forest as ranging from pure totara, to totara - matai, to totara - matai - kahikatea, to dense mixed podocarps. The relative proportions of totara, matai, and kahikatea appear to be due to edaphic features such as fertility and drainage. In dense mixed podocarp forest, totara is confined in small populations to optimal sites such as terraces and ridges.

The podocarps have differing nutrient, light, and disturbance regime requirements and these factors work together to partition the environment into optimal areas for the regeneration and persistence of each species. Totara dominated stands require high light to initiate and capture a high fertility site, and relatively free-draining

fertile soils to remain dominant. Sub-optimal totara sites will see the dominance of other species such as rimu. Totara and kahikatea dominate in catastrophically disturbed areas, miro responds to medium levels of disturbance such as tree fall, and rimu dominates in areas subject to continual disturbance such as canopy collapse.

Regeneration of lowland totara dominated forest is seen to be a consequence of seedling dispersal to preferred microsites, and disturbance history. The broad scale forest pattern is determined by the level of disturbance and the finer scale pattern of tree distribution is a result of light levels, parent and perch trees, and edaphic properties. There is no evidence that totara dominated stands are older than first generation, indicating that periodic catastrophic regeneration is required to re-initiate stands. The alteration of the natural disturbance regime by humans may pose problems for the future of lowland totara.

There is no evidence that totara forest regenerates under a senescing totara canopy. Presently protected areas are therefore likely to undergo floristic composition change away from totara/matai/kahikatea in the absence of disturbance. A landscape management plan is proposed as a mechanism for appropriate land use using ecological principles at catchment scale and to provide adequate areas for the long-term survival of totara dominated forest in a fragmented landscape.

New Zealand's natural environment has been radically altered with the invasion of humans, introduced weeds and pests, and alteration of the natural disturbance regime. Restoration and revegetation are therefore options for the future survival of lowland totara in a fragmented landscape. Silvicultural plantations can provide timber (totara heartwood being highly prized), income, and seed sources for regeneration. Land values such as water and soil quality will also benefit from artificial plantations. Stand spacing and age structure is described and can be used in the future when revegetation projects have the aim of approximating natural stands.

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CHAPTER ONE
INTRODUCTION

1.1 GENERAL INTRODUCTION

Lowland totara (*Podocarpus totara* G.Benn. ex D.Don., Connor & Edgar 1987) is one of New Zealand's largest trees, being bettered in girth only by kauri (*Agathis australis* Salisb.) and topped in height by kahikatea (*Dacrycarpus dacrydioides* A.Rich.). Lowland totara dominated stands form a distinct forest type within the 'dense lowland podocarp' classification (McKelvey 1963, 1973, Nicholls 1976, Wardle 1977). To the Maori people lowland totara is a significant tree due to its size and outstanding properties for canoe building and carving.

Since the first fires associated with early Polynesian settlers some 800-1000 years ago (McGlone 1983b) burning, logging, and clearing for settlement have substantially reduced or modified New Zealand's forests. The extensive deforestation that accompanied Polynesian and European settlement of New Zealand has had a disproportionately high impact on lowland podocarp forest, with the majority gone and the remaining forests surviving in isolated remnants of generally small size. Lowland podocarp forest is significantly under-represented in New Zealand's reserve system and there are very few examples of totara dominated forest remaining in New Zealand (e.g. Park & Walls 1978).

There is growing interest in the conservation and restoration of totara dominated lowland podocarp forests in New Zealand. However, our knowledge of this endemic forest tree species is surprisingly limited, particularly with respect to factors that influence its regeneration, dominance and persistence at a site, and stand history. Because most remaining areas of lowland totara are small isolated remnants it is important to assess whether these areas will maintain themselves as totara dominated communities and to determine if any management intervention is required for the future survival of this species in a fragmented landscape. Before addressing the future of lowland totara and its restoration, an understanding of the species' ecology is required.

Integrated landscape management provides for the integration of forest remnants in a fragmented landscape and ensures the survival of threatened species in the future. All ecological and social aspects are taken into account in the development of community-based landscape plans. A new land ethic is rapidly emerging where land users are recognising the integrated nature of the landscape and implications of their land management practices. Restoration and landscape ecology are new and exciting fields, requiring a cooperative effort between scientists and the public.

1.2 OBJECTIVES AND OUTLINE OF THESIS

There are two main aims of the thesis:

1. To elucidate the ecology of *Podocarpus totara*
Research approach:
- Investigate literature concerning the ecology of *Podocarpus totara* and identify areas of knowledge which require further research.
- Evaluate the current distribution and ecological niche of *Podocarpus totara* dominated communities in South Island, New Zealand. Determine potential pre-deforestation extent based on historical records and landform/vegetation relationships.
- Use rapid mapping techniques to determine stand history, regeneration requirements, forest associations, stand development and structure.

2. To assess the future survival of *Podocarpus totara* in fragmented landscapes
Research approach:
- Determine whether the current floristic composition and structure of totara dominated remnants will be sustained in the future or whether new areas must be provided for regeneration so as to ensure the persistence of lowland totara.
- Discuss and review the restoration of *Podocarpus totara* dominated forest, management options, and the long term survival of this species in a fragmented landscape, based on ecological knowledge.
- Produce an example of an integrated landscape management plan to allow for sound land use practices and forest regeneration.

To fulfill these main aims, various aspects of lowland totara are studied. Part One of the thesis contains a general introduction to lowland totara, Part Two investigates the ecology of lowland totara, and Part Three investigates the future survival and conservation of lowland totara in a fragmented landscape. Each chapter addresses specific objectives and research questions. The structure of the

thesis, and the objectives of each chapter, are outlined below.

PART ONE - Introduction to lowland totara

Chapter Two contains a full review of the literature relating to lowland totara. Gaps in the knowledge base are identified and used to determine the research approach of the thesis. The objectives of this chapter are:

- To review the literature concerning lowland totara and to identify gaps in the knowledge base.

Chapter Three details study site selection, data collection, and tree ageing methodologies. The objectives of this chapter are:

- To ensure adequate coverage of geographical location and climate in the northern half of South Island.
- To ensure adequate coverage of a range of landforms and soils.
- Ensure adequate coverage of all lowland totara forest types and development status.

Chapter Four outlines the distribution and niche requirements of lowland totara. Data on current distribution, study site climate and landform, and study site soils are given. The objectives of this chapter are:

- To determine the distribution of lowland totara in terms of altitude,
- To determine the distribution of lowland totara in terms of annual rainfall.
- To determine the climate in which lowland totara occurs in South Island,
- To determine if lowland totara is confined to distinct landforms in South Island.
- To determine the range of soils lowland totara occurs on,
- To investigate the relationships between soil type, landform, and disturbance regime.

PART TWO - The ecology of lowland totara

Chapter Five discusses the disturbance history of the study sites and determines the importance of disturbance for the regeneration of lowland totara. The objectives of this chapter are:

- To determine whether disturbance is a significant factor in the regeneration of lowland totara forest,
- If so, what are the disturbance types and scale?

Chapter Six provides in-depth descriptions of lowland totara dominated stands. Study site forest types, descriptions, and age class frequencies are given. The objectives of this chapter are:

- To determine what forest types occur and to determine if previous classifications are adequate in describing lowland totara forest types.
- To describe the structure of lowland totara forest in terms of number, basal area, and species composition.
- To describe the vertical structure of lowland totara forest.
- To investigate the age structure of the stands.

Chapter Seven investigates seedling ecology. Studies on seedling distribution, spacing, and establishment are presented. The objectives of this chapter are:

- To elucidate podocarp seedling ecology through an investigation of seedling position, spatial description, and light level requirements.
- To investigate the relative roles of both angiosperms and podocarps (parent trees and otherwise) in the position of seedlings.

Chapter Eight investigates the spatial structure of lowland totara dominated stands. Analyses are applied to determine patterns, processes, and associations. The objective of this chapter is:

- To investigate the spatial structure of lowland totara dominated stands. Are adult tree distributed at random? If not, what are the patterns, processes, and associations? Are the stands even-aged and does this correlate with the disturbance regime?

Chapter Nine details temporal patterns in stand growth through an investigation of ring widths and stand growth. An understanding of the temporal development of totara dominated stands will help in the prediction of future stand structure and the classification of the forest type. The objective of this chapter is:

- To investigate stand growth through time via a study of ring widths.

To fulfill this objective, two further research questions are addressed:

- Does lowland totara dominated forest develop along a predictable pathway of stand growth?
- If so, can models be generated to aid in predicting the future development of lowland totara dominated stands?

Chapter Ten is an overview of the ecology of lowland totara based on the studies performed in Part Two. With an understanding of the ecology of lowland totara, one can then address the future survival of this species.

PART THREE - Conservation of lowland totara in a fragmented landscape

Chapter Eleven contains a review of fragmentation literature as well as an example of fragmentation in an area which had extensive totara forest (Banks Peninsula). Data on forest reduction is presented. The objectives of this chapter are to:

- Review and discuss the charactoristics and consequences of fragmentation for both plants and animals.
- Identify threats to remnants, management options, and research priorities.
- Identify consequences of fragmentation which are relevent to the future survival of lowland totara.
- Provide an example of fragmentation using Banks Peninsula as a case study.

Chapter Twelve presents an integrated landscape plan to provide for the regeneration of lowland totara in the future based on regeneration requirements for an area in Banks Peninsula. A questionnaire of landowner attitudes is presented as well as options for landowners to provide for the future regeneration of lowland totara. Other landuse issues such as soil protection are discussed. The objectives of this chapter are:

- To provide a case study of one representative catchment on Banks Peninsula.
- To determine the suitability of the integrated landscape management approach at the catchment level for improving the biological conservation of lowland totara while allowing for other land uses.

Chapter Thirteen contains the concluding discussion concerning the ecology of lowland totara - its distribution, regeneration, and future survival in a fragmented landscape.

While lowland totara forest has been severely reduced in extent, every effort was made in the present study to sample as many remnant stands as possible to ensure adequate coverage of forest types and geographical position. Study sites are from the northern half of South Island and so results are only directly applicable to lowland totara in South Island. However, many similar stands occur in North Island and it would be reasonable to expect that similar conclusions could be drawn for North Island totara remnants.

1.3 CONVENTIONS

Latin names will be used in the literature review section as it deals with specific species. Common names will be used throughout the remainder of this thesis - for full botanical names refer to Appendix One.

Colours used to represent the main podocarp species in figures are standardised for ease of graph interpretation and consistency; lowland totara (red), Hall's totara (maroon), matai (green), kahikatea (blue), miro (pale yellow), rimu (yellow), angiosperms (grey).

CHAPTER TWO
LITERATURE REVIEW

2.1 INTRODUCTION

2.1.1 General introduction

The objectives of this chapter are to review the literature concerning lowland totara and to identify gaps in the knowledge base. The research approach of this thesis can then be focused on areas requiring further investigation.

In this section, published papers and books, student theses and dissertations, and unpublished reports (largely of the Forest Research Institute) are reviewed. Readers should consult the original publications for full details of the work quoted. Some of the unpublished reports and student dissertations represent only preliminary studies.

The review is divided into four sections: vegetative morphology and growth, reproductive biology, timber utilisation, and population dynamics. Literature relating to restoration is reviewed in subsequent chapters which deal with this topic specifically. Only literature concerning *Podocarpus totara* and the closely related *Podocarpus hallii* is reviewed; for a full review of all four *Podocarpus* species see Ebbett & Norton (in prep.).

2.1.2 Taxonomy

The genus *Podocarpus* (Podocarpaceae) was first described by L'Heritier in 1807, with the New Zealand members being named between 1825 and 1889 (Allan 1961). The last thirty years has seen extensive scrutiny of the New Zealand Podocarpaceae, as reported by Edgar & Connor (1983) and Connor & Edgar (1987), with three of the seven taxa assigned to *Podocarpus* (Allan 1961) being transferred to other genera. Thus for New Zealand, *Podocarpus sensu stricto* consists of four species; *P.acutifolius* Kirk, *P.hallii* Kirk, *P.nivalis* Hook, and *P.totara* G.Benn. ex D.Don. More recently a stable hybrid between *P.totara* and *P.acutifolius* was

recognised and described by P.Wardle (1972) as *P.totara* var. *waihoensis* (Westland totara). De Laubenfels' recognition of three generic divisions of *Podocarpus* is supported by the distribution of flavenoid glycosides (Markham et al 1985). This chemotaxonomic method also confirms the parentage of *P.totara* var. *waihoensis* (Webby, Markham & Molloy 1987).

The New Zealand species of *Podocarpus* are included in section Eudopodocarpus subsection D (Bucholtz & Gray 1948) together with *P.lawrencei* (from Tasmania and SE Australia), *P.gnidioides* (New Caledonia), and *P.nubigenus* (Argentina, Chile). *P.gnidioides* is the only species of this subsection that is considered threatened due to its restricted range (Farjon, Page & Schellevis 1993).

2.1.3 Hybridism

The endemic New Zealand *Podocarpus* species readily hybridise in the wild producing an array of intermediate forms. Cockayne (1923) listed *P.hallii* x *totara*, Cockayne & Allan (1934) described several hybrid groups: *P.acutifolius* x *hallii*, *P.hallii* x *nivalis* which produces forms that mimic the bushy *P.acutifolius*, *P.hallii* x *totara* which was named *P.loderi*, and *P.acutifolius* x *nivalis* which was named *P.acutinivalis*, suggesting that hybrids in the latter group contained *P.hallii* "blood" due to the presence of *P.hallii* leaf characteristics, implying the involvement of a third parent. What Cockayne (1932) once considered *P.nivalis* var. *erectus* (*P.nivalis* x *hallii*)was later considered to be a form of *P.hallii*. Cockayne(1932) draws attention to the small trees of south Westland which he at first believed to be a new species of *Podocarpus* but which he later considered to be an epharmone (or environmentally-induced variety) of *P.acutifolius* - a caution created by his earlier experiences with *Podocarpus* epharmony.

There is strong evidence for introgressive hybridisation between *P.acutifolius* and *P.totara* (Wardle 1972, Webby et al 1987). Work has shown that this cross has produced a hybrid swarm and a stable, uniform hybrid, namely the small trees of south Westland formally described as *P.totara* var. *waihoensis* Wardle. The characterisation of *Podocarpus* hybrids using flavenoid markers is discussed by Webby et al (1987), who show that all of the New Zealand species hybridise with each other with the added complication of backcrossing with a third parent. Of interest in their paper is the occurrence of hybrids well beyond the geographical limits of some parent species e.g. *P.hallii* x *nivalis* hybrids occur on Banks Peninsula whereas one of the parents, *P.nivalis*, does not.

2.2 VEGETATIVE MORPHOLOGY AND GROWTH

2.2.1 Description

Section *Podocarpus* is the typical section of the genus *Podocarpus* with leaves either with hypoderm, hypodermal fibres or well-developed transfusion tissue (Griffin 1907, Hora 1980). The receptacle is typically well developed, more or less fleshy to leathery (Hora 1980). Botanical descriptions of the New Zealand *Podocarpus* species are given by Allan (1961), Salmon (1980), and Poole & Adams (1990) and are summarised below (see Figure 2.1). Seedling morphology is discussed by Phillipson & Molloy (1990). The development of leaves in *P.totara* is discussed by (Griffin 1907) and notes on the morphology of *P.totara* and *P.hallii* are presented by Gardner (1990).

• *P.acutifolius* ("sharp-leaved"). Erect, shrub or small tree reaching 10m, leaves acuminate and pungent (Poole & Adams 1990), branchlets slender (Salmon 1980). Found from Marlborough Sounds to South Westland, being common in the Nelson Lakes area (Salmon 1980).

• *P.hallii* (Hall's totara, mountain totara). Tree reaching 20m, bark thin and stringy (Poole & Adams 1990). Trunk up to 1.25m. Found from sea level to c. 600m but more common than *P.totara* at altitudes above 480m (Salmon 1980). Leaves longer than *P.totara* and seed acute rather than rounded (Hora 1980).

• *P.nivalis* (snow totara). Prostrate shrub with thick, coriaceous leaves (Poole & Adams 1990) found in sub-alpine and alpine regions. Procumbent to prostrate or buried stems that can form layered colonies extending as much as 16m downhill from the point of establishment (Wardle 1991). Semi-erect bushes growing about 1m tall occur on level ground at lower altitudes (Wardle 1963). Bud scales are modified leaves which may persist several years, leaves persist 5-9 years (Wardle 1963).

• *P.totara* (Lowland totara). Tree reaching 30m or more, bark thick, stringy and furrowed, leaves coriaceous with juvenile longer than adult (Poole & Adams 1990). Found from sea level to c. 600m. In its early stages totara forms a bushy, spreading tree and aquires a massive trunk (up to 3m D.B.H.) and branches that bear dense foliage as it gains height. Enormous roots spread out over the ground at the base of the trunk (Salmon 1980). Seed mostly solitary, more or less globose (Hora 1980).

• *P.totara* var. *waihoensis* (Westland totara) Tree rarely exceeding 12m with narrower more acute leaves than *P.totara* (Poole & Adams 1990). In closed forest on fertile alluvium it forms small-leaved, moderate-sized, single-stemmed trees with spreading canopies, thus resembling *P.totara*. On forest margins, in the open, and on infertile sites it forms smaller, multi-leadered trees often with decumbent lower branches, thus resembling *P.acutifolius* (Phillipson & Molloy 1990).

2.2.2 Vegetative propagation

Except for artificially struck cuttings of *P.totara* in nursery conditions, the natural establishment of dispersed vegetative fragments is unknown for the Podocarpaceae (Preest 1963).

2.2.3 Provenance and genetic variation

Bergin & Kimberley (1992) found early growth of *P.totara* seedlings to be highly correlated with germination rate after sowing; seeds germinating earlier has greater growth. Height growth in 2yr old *P.totara* seedlings became negatively correlated with provenance latitude, eight of the fastest growing provenances being from widely scattered North Island localities and one from the northern South Island. They suggested that genetic factors correlated with mean summer temperature of the seed source locality were beginning to predominate. Stem form and branch length also varied but this did not relate to any provenance site variables; leaf size and foliage colour were not variable between provenances (Bergin & Kimberley 1992).

One of the most comprehensive studies of genetic and provenance variation in *P.totara* is that of Hawkins (1988) who presented the results of seedling nutrition, temperature, and isozyme analysis experiments. Hawkins (1988) found no correlation between optimal growing temperature and climate of seed origin for seven *P.totara* provenances but did note a correlation between *P.totara* frost tolerance and climate of origin.

Slui (1988) found *P.totara* provenances to exhibit considerable variation in phenological characteristics such as height, total growth, and stem to leaf ratios of seedling dry matter production. Relative growth rates were all significantly correlated to climatic variables, indicating a strong provenance differentiation. Slui (1988) suggests that this physiological specialisation within each provenance is

keyed to a permanent genetic adjustment to the rainfall and temperature regime at their seed source.

Frost hardiness of *P.totara* seedlings was found to be positively correlated with the altitude of provenance origin (Hawkins et al 1991). Isozyme analysis of four variable loci in new foliage of *P.totara* showed allele frequencies at one locus to be significantly correlated with provenance frost hardiness, suggesting variation is due to genetic factors rather than being environmentally induced (Hawkins et al 1991). Hawkins (1988) found seven of ten variable loci in *P.nivalis* to be correlated with one or more environmental variables (e.g. precipitation, altitude, mean annual temperature).

Isozyme analysis of *P.totara* found a genetic differentiation among populations of 36.2% compared with the conifer average of 6.8%, although 33.9% of the genetic diversity was attributable to differences between varieties *totara* and *waihoensis* (Billington & Sweet in prep.). Mean number of alleles per locus and percentage polymorphism was found to be largest in *P.hallii* (Billington & Sweet in prep.). The greater genetic variability found in *Podocarpus* species may be due to differences in chromosome number, degree of inbreeding, or amount of hybridisation (Hawkins, 1988). Hawkins (1988) suggests that this variability would enable *Podocarpus* species to react more quickly to selection pressures.

2.2.4 Drought and freezing resistance

Studies on the effect of drought on indigenous plants showed *P.totara* saplings (up to 2m height and 10cm D.B.H.) and large trees (over 50cm D.B.H.) to be apparently unaffected (Atkinson & Greenwood 1972). Innes & Kelly (1992) observed the production of shorter than normal leaves in *P.totara* during the 1987-89 drought on Banks Peninsula. *P.totara* was susceptible to drought and was seen to be a 'drought avoider' by growing in wetter sites and maintaining a high internal water potential (Innes & Kelly 1992).

Freezing resistance studies by Sakai & Wardle (1978) and Sakai, Paton & Wardle (1979) show *P.totara* to be moderately hardy, with leaves, buds, and twigs surviving at -7 ^{0}C. Hawkins et al (1991) suggest that frost hardiness in *P.totara* is due to genetic differences (see above section). Hawkins (1988) states that *P.nivalis* has developed a greater tolerance to cold than *P.totara* or *P.hallii* due to the colder climate of the last 2,000,000 years but optimal temperature for growth and photosynthesis has not been modified.

Death of *P.totara* foliage following severe frost was noted in Southland (D.Norton pers.comm.) although trees subsequently recovered. Some mortality was seen in *Dacrydium cupressinum* and *Dacrycarpus dacrydioides*. Late and early frosts during the short growing season may cause mortality to *P.totara* seedlings under *Leptospermum* scrub (Beveridge 1973a).

2.2.5 Life span

Salmon (1980) states that *P.totara* often reaches 800 years old and cites the Pouakani Totara in the King Country as reputedly being 1800 years old. A wood sample from the middle of a circa 3m diameter *P.totara* in Whirinaki Sanctuary has been radiocarbon dated at 898 ± 28 years (Ebbett 1992). The innermost heartwood of the bole was rotten and so this is a minimum age. Hinds & Reid (1957) suspect a life span of up to 1000 years for *P.hallii*. Wearing (1995) states that *P.hallii* is long-lived in Central Otago, reaching ages of 900 years or more. However, average life span is likely to be 600 - 800 years.

2.2.6 Seedling growth

Ebbett (1992) found three year old *P.totara* seedlings increased in height by 220% in the glasshouse environment with 25% of full sunlight. Light levels of this magnitude are only found within canopy gaps in dense lowland podocarp forest and so are considered to be relatively high. Both *P.totara* and *D.dacrydioides* showed a significantly greater height growth increase in high light levels than *Prumnopitys ferruginea, P.taxifolia,* and *Dacrydium cupressinum*. Slui (1988) conducted provenance trials on *P.totara* seedlings and found that genetic based adaptations which accentuate height growth seemed to have developed in seedlings from provenances whose seed source is located in areas of high summer temperatures. As *P.totara* is a light demander, Slui (1988) suggests this result is not unexpected as seedling height growth is an important factor in helping it to compete successfully.

Hawkins & Sweet (1989a) found experimentally grown *P.totara* seedlings to increase dramatically in total weight between 21 and 27°C. All seedlings died or performed poorly in the 35/30°C temperature regime. Hawkins & Sweet (1989b) found *Dacrydium cupressinum, P.totara,* and *Dacrycarpus dacrydioides* had a linear growth response to increased nutrition (N.P.K) with *P.totara* having the steepest growth response. This may indicate the competitive advantage of *P.totara* on more fertile sites due to its greater nutrient uptake ability.

2.2.7 Height growth

Molesworth (no date) notes the growth of planted *P.totara* trees; a 39 year old tree had increased in height by 14cm per annum, a 25yr old tree by 10cm per annum, and an 8yr old tree in a sunny position by 25cm per annum. Katz (1980a) records a 20cm per annum height increase in *P.totara* saplings.

Bergin and Kimberley (1992) found a positive correlation between height growth of *P.totara* seedlings and mean summer temperature in provenance trials but no significant correlation between height growth and altitude. Hawkins (1988) suggested that the high growth rates of *Dacrycarpus dacrydioides* and *P.totara* seedlings, compared to *Dacrydium cupressinum*, may be due to the larger seed size and hence nutrient reserves or the superior ability of these species to utilise available nutrients.

2.2.8 Diameter growth

Only a few diameter growth studies were located for *P.totara*: 3 year old seedlings showed a diameter growth of 0.40-2.55mm (mean=1.12mm) per annum under light levels ranging from 2-30% of full sunlight (Ebbett & Ogden 1998), 8 year old saplings in a sunny position grew on average 0.95-1.11mm in diameter per annum (Molesworth no date), and 39 year old trees in damp, shady conditions grew on average 1.4mm per annum (Molesworth no date). Katz (1980a) records a diameter increase of 2.4mm for saplings (7.5-12.4cm D.B.H.) and 4.3mm for small trees (12.5-17.4cm D.B.H.) from a 20 year study in Whirinaki Forest Park, also described by Cameron (1960a).

2.2.9 Seasonal growth pattern

Beveridge (1973a) states that height growth in *P.totara* occurs in one or two short flushes, each lasting for a period of two to three weeks before hardening of the foliage and formation of a resting bud. Ebbett & Ogden (1998) found that 3 year old *P.totara* seedlings grown in various light levels in the forest exhibited a seasonal response. Seedlings grown in 5% of full sunlight showed peak seasonal height growth corresponding to the peak in temperature and sunlight (summer) whereas seedlings in 30% of full sunlight showed a marked seasonal response to high rainfall and humidity (winter). Seedlings grown in intermediate light levels did not exhibit seasonal variation in height growth.

2.2.10 Root growth

Foweraker (1929) observed that *P.totara* responds to silting by producing another tier of roots above the original primary root system and that this second tier of roots is commonly found in old silted stands such as those on the river flats of Westland. This ability is inherited from *P.acutifolius*, a parent of *P.totara* var. *waihoensis*, which Foweraker (1929) described as *P.totara* (Phillipson & Molloy 1990). Wardle (1963) found *P.nivalis* buried stems and roots growing 16m downhill from the aerial parts, an indication of this species' role in soil stabilisation.

Forest and glasshouse grown *P.totara* seedlings appear to maintain their root/shoot weight ratio irrespective of the light level under which they are being grown (Ebbett 1992). Hawkins & Sweet (1989a) found that root/total weight ratio does not change significantly with a change in temperature regime. However, at low levels of nutrition *P.totara* shows a significantly greater proportional allocation of dry matter to the roots (Hawkins 1988, Hawkins & Sweet 1989b). The proportionally higher root weight and high plasticity of allocating resources to roots at lower levels of nutrition is a common response in plants characteristic of a stressful environment, such as colonising coastal sand dunes (Hawkins 1988, Hawkins & Sweet 1989b). *P. totara* and *Dacrycarpus dacrydioides* showed a greater change in root production than *Dacrydium cupressinum* due to increased nutrition. *P.totara* exhibited higher potassium and calcium levels due to a greater uptake efficiency of these nutrients (Hawkins 1988, Hawkins & Sweet 1989b).

2.2.11 Root nodules

The literature concerning Podocarpaceae root nodules has been reviewed by Bond (1967) and Hawkins (1988) and only those papers relevant to New Zealand's *Podocarpus* species will be discussed here. The fine roots of the podocarps are studded with small nodules which appear to be peculiar to the Podocarpaceae and Arucariaceae. Transverse constrictions arise on young rootlets before the true nodules arise in longitudinal rows between these constrictions (Baylis, McNabb & Morrison 1963). This alignment, together with a small and uniform size, distinguishes them from the root nodules of legumes and other dicotyledons. Baylis et al (1963) states that *P.hallii* has some of the largest nodules within the Podocarpaceae (0.8-1.4mm diameter). Each nodule is a modified lateral root and arises in the pericycle outside a metaxylem group, ruptures the endodermis and crushes the underlying cortex. The cortex lignifies and the cytoplasm and nuclei disappear (Baylis et al 1963).

In *P.totara* restricted apical growth results in the young nodules being produced each year completely inside the old ones (Yeates 1924). In other species, such as *Dacrycarpus dacrydioides*, the stele of the nodule is long and it is sufficiently extended each year for the new cortex to be carried clear of the old, occasionally accompanied by branching (Baylis et al 1963).

The cause of nodulation in the Podocarpaceae has been debated for some time. Spratt (1912) claimed that Podocarpaceae nodules are produced by the infection of the meristematic tissue of the young root by the bacteria *Pseudomonas (Rhizobium) radicicola*, the same as is found in legumes. Her observations received some support (Phillips 1932) but most researchers have recognised a phycomycetous fungus as the most prominent organism in the nodule cortex (Yeates 1924, Saxton 1930, Baylis et al 1963). Spratt (1912) and Phillips (1932) did, however, record the occasional fungal hyphae in the empty outer cortical cells which they thought may have been of a mychorrhizal nature. Baylis (1969) showed that vesicular-arbuscular mychorrhizas were created in *P.totara* after inoculation with phycomycete spores. Johnson (1973) shows that *P.hallii* becomes mycorrhizal after inoculation with *Acaulospora laevis* fungi but not other species.

Saxton (1930) suggested that in habitats where Leguminosae are present and the soil is full of *Rhizobium* bacteria, the latter may invade the nodule following mycorrhizal invasion and may even succeed in supplanting the fungal hyphae in the central tissue. Baylis et al (1963) state that nodules containing no fungal mycelium appear abundantly on seedlings raised in sterile culture and no bacteria could be demonstrated in developing nodules. They suggest that bacteria outside the root may play a part in nodulation as the producers of a growth substance or macerating agent which assists rupture of the cortex.

The physiological significance of *Podocarpus* root nodules has been investigated by Spratt (1912), Yeates (1924), Baylis et al (1963), and Bond (1967). Yeates (1924) provides evidence that the nodules of *Podocarpus* act as water storage tissues, reporting large cushions of nodules in *P.hallii*. Significantly greater vigour and growth was noted in mycorrhiza affected *P.totara* (Baylis et al 1963). Bond (1967) grew one *P.nivalis* seedling in nitrogen-free soil and concluded that the new season growth was attributable to the nitrogen in the plant initially, rather than attributing the root nodules with extensive N-fixation. He also reviews 15N studies which provide the main evidence for the occurrence of nitrogen fixation in nodules, although they are by no means conclusive. Hawkins (1988) records significant improvements in *P.totara* seedling growth and enhanced uptake of phosphorous

and nitrogen due to mycorrhiza infection.

2.2.12 Injurious agencies

Dieback of both *P.hallii* and *P.totara* has been noted by Beveridge (1983), Wardle (1978), and Wardle et al (1983). *P.totara* is considered to be of low palatability to browsing animals such as deer, goats, cattle, and possums (Jane 1983), but seedlings may be damaged if more palatable food is scarce. Possums are known to feed in winter on the previous season's growth in the crowns of *P.totara* trees (Beveridge 1983).

In a study on the effect of control of brushtail possums, Pekelharing and Batcheler (1990) document severe browsing damage to *P.hallii* in Westland. They indicated that possum control should be conducted at least every decade to maintain low levels of browse damage to palatable species. Approximately 20% of the dry weight gut content of possums in the Waihaha area is *P.hallii* (Department of Conservation unpub. data). Dead *P.hallii* on the higher slopes of Banks Peninsula, where possums are abundant, show an exposure factor - sheltered parts of the crowns tend to be healthier than the windward parts (Wardle 1978). While possums may be a cause, the mortality has also been pronounced where possums are absent (e.g. *P.hallii* Wardle 1978).

P.totara seedlings are subject to defoliation by insects, mainly tortricid and geometrid caterpillars (Beveridge 1973a). Beveridge (1983) states that seedlings of all Podocarpaceae species growing in well-lit situations are liable to stem lesions caused by egg-laying cicadas, and that these lesions are often entry points for the larvae of the striped longhorn beetle (*Navomorpha* sp.). In Westland, the buds of moribund *P.hallii* trees have been found to harbour the caterpillar of *Ctenopseustis obliquana* (Wardle 1978, Wardle et al 1983). The incidence of death may also be related to soil conditions, stands on steep mountain slopes being heavily afflicted, those on the gley podzols of ancient moraines and on fertile alluvial soils of valleys usually healthy (Wardle 1978).

The New Zealand endemic mistletoe *Ileostylus micranthus* parasitises both *P.totara* and *P.hallii*, particularly in Northland, Nelson, and Southland. Eight percent of *Ileostylus micranthus* herbarium sheets were recorded as parasitising on *P.totara* or *P.hallii* (D.Norton & P.J.de Lange unpub.data). Shaw (1983) suggests that initial minor damage from tropical cyclones and storms may be followed by a later dieback and general deterioration of stand structure.

2.3 REPRODUCTIVE BIOLOGY

2.3.1 Sex distribution

No information or data concerning the sex distribution of *Podocarpus* species was located, but all species are dioecious.

2.3.2 Reproductive development

McEwen (1988) outlines the reproductive cycles of both *P.totara* and *P.hallii*. During winter club-shaped shoots on male trees contain minute cones which break bud in late October and shed pollen in November to December. Strobili occur singly or in groups with *P.totara* having up to four and *P.hallii* five on a single peduncle (Salmon 1980). Ovules are single or in pairs on a receptacle set on a short stalk, appearing towards the base of the new season's growth shortly before pollination. *P.totara* has a reduced female cone with one or two ovules in each (Sporne 1965). Development is rapid - ovules are fertilised two to three months after pollination and fruit ripens by March, or up to two months later at higher altitudes. The receptacle ripens to a bright red colour while seed and stalk remain green. Some trees have seed with orange or yellow receptacles.

In some cases a second flushing occurs in late summer (*P.totara*) or autumn (*P.hallii*) and a second crop of new ovules are produced on female trees. Club-shaped shoots also burst into a second crop of male cones. Seed is occasionally produced in spring this way but may lack embryos. *P.hallii* have longer and narrower seeds and the cones are set on longer stalks than those of *P.totara* (McEwen 1988). *P.hallii* seed is often pointed whereas lowland totara seed is ovoid (Bergin & Kimberley 1992). Bergin & Ecroyd (1987) found *P.totara* seed to average 5mm in length and *P.hallii* 7.6mm. As no overlap was observed in seed size, seeds of around 6mm length are likely to be hybrids.

2.3.3 Pollen grains

The pollen grains of all four *Podocarpus* species are described by Cranwell (1940). *P.hallii* and *P.totara* are somewhat similar but *P.hallii* tends to be larger and less rounded. *P.acutifolius* and *P.nivalis* are also similar to each other but *P.acutifolius* pollen is smaller and has a thinner exine. *P.nivalis* is similar to the other three but generally has a much larger grain with a thicker exine (Cranwell 1940). Pocknall

(1981) presents a key for pollen identification which separates the *Podocarpus* species into a group but states that further identification is difficult. Pocknall (1981) disagrees with Cranwell's assertion that *P.nivalis* grains are larger, and shows that *P.totara* var. *waihoensis* pollen grains resemble both parents.

2.3.4 Reproductive periodicity

A ten year study of *P.totara* seedfall by Beveridge (1973b) indicates an annual seed crop which fluctuates in abundance. Mature high forest trees rarely have a heavy seed crop, seeds being more abundant on pole-sized trees of second-growth stands (Beveridge & Smale 1981). The reason for this variability in seeding is unclear. *P.totara* and *P.hallii* seed collection methods are outlined by Beveridge & Smale (1981) and Bergin & Ecroyd (1987).

2.3.5 Seed dispersal

All New Zealand Podocarpaceae seeds are moist and heavy when ripe, filled with oily endospermous food reserves. *Podocarpus* species have a succulent fleshy receptacle which the seed is perched on, with seed and receptacle being shed together (Preest 1963). The attractiveness of the fleshy receptacle to many forest birds makes these species well suited to bird dispersal. They are also suited to dispersal by water but not by wind. Most seed falls directly under the parent tree (Preest 1963). In a study of podocarp regeneration following the 1886 Tarawera eruption, Burke (1974) found *P.hallii* seedlings no further than 58m from parent trees whereas *P.totara* seed had been dispersed 4.8km. Site factors, rather than the influence of birds on dispersal, was suggested for the difference in the observed distributions.

The importance of forest birds as seed dispersers is discussed by Clout & Hay (1989) although not specifically for *Podocarpus* species. Robertson & Hackwell (1995) show that native birds play an important role in the succession of *Dacrycarpus dacrydioides* forests in South Westland, as birds are the principal agents for long distance seed dispersal of both the shrub species and kahikatea itself. Preest (1963) states that podocarp regeneration presumed to be the result of bird dispersal can be seen many kilometers from the source, frequently associated with suitable perching places. McEwen (1978) discusses the habits of the new Zealand wood pigeon (*Hemiphaga novaseelandiae novaeseelandiae*). Birds are known to move from place to place follwoing the supply of fruit. They also migrate seasonally to escape harsh winter conditions or to find fruit.

The importance of hardwood (angiosperm) tree species on bird behaviour is recognised by Preest (1963), Beveridge (1973) and McEwen (1978). In a study of cyclic podocarp regeneration, Beveridge (1973) shows that hardwood trees develop in tree-fall gaps and grow into suitable perch trees. Podocarp seedlings are recruited under the hardwood tree from bird dispersed seeds and grow into saplings as the hardwood tree gradually thins and dies.

Likely extant native species for *Podocarpus* seed dispersal include tui (*Prosthemadera novaeseelandiae*), bellbird (*Anthornis melanura*), and kereru (*Hemaphaga novaeseelandiae*) (Beveridge 1973a). McEwen (1978) suggests that *P.totara* bears its seed too sparsely for *Hemaphaga novaeseelandiae* to gather sufficient quantities without too much effort, especially in the season when the favoured *Prumnopitys ferruginea* fruit are ripe. Wells (1972) suggests that bellbirds, which are common in adult trees when the seed is ripe, are effective dispersers of *P.hallii* seed. Beveridge (1973a) also lists four introduced bird species which may act as minor dispersers at the forest edge - blackbird (*Turdus merula merula*), thrush (*Turdus philomelos*), Indian mynah (*Acridotheres tristis*), and starling (*Sturnus vulgaris vulgaris*).

2.3.6 Seed predation

Beveridge (1973b) states that in calm weather few seeds of *Dacrydium cupressinum*, *Dacrycarpus dacrydioides* or *Podocarpus totara* fall with ripe receptacles attached as many seeds and receptacles are eaten in the tree crowns, possibly by possums (Jane 1983). Beveridge & Smale (1981) and Jane (1983) discuss seed predation and note that brown and ship rats may eat *P.totara* receptacles but not the seed.

Beveridge & Smale (1981) recorded that up to 40% of *P.totara* seed falling from a tree with a light seed crop was destroyed by yellow-crowned parakeets who crack the seed open and eat the inner contents. Powlesland (1987) shows that Podocarpaceae species (including *P.totara* and *P.hallii*) constitute 14% of the kokako (*Callaeas cinerea wilsoni*) diet in Northland.

2.3.7 Seed germination and viability

P.totara seed is collected in April/May (N.C.W.C. 1976) and the fleshy receptacle removed. Seed can then be stored for 6-18 months in moist cool conditions although germination is more consistent if sown in autumn immediately after collection (F.R.I. 1980). Herbert (1976) discusses the collection of seed contained in forest litter, the effect of depth of litter on germination, and methods of preparing

seed beds. Bergin & Ecroyd (1987) show that winter litter collections showed good germination whereas early autumn or fresh fallen seed collections showed poor germination. Germination of *P.totara* seed is not sensitive to drying conditions although a cold period is required (Fountain & Outred 1991).

Beveridge & Smale (1981) note that most *P.totara* seed germinates in spring or autumn, 6-12 months after seedfall, although dormancy periods of up to two years were observed. Bergin & Ecroyd (1987) noted *P.totara* seed germination as early as four weeks after sowing. Trials conducted at the Forest Research Institute saw half of the *P.totara* provenances germinating within six weeks of sowing with the remainder germinating within ten weeks (Bergin & Kimberley 1992). A second germination flush was seen six months later. Hawkins (1988) suggests that *P.totara* seeds from provenances of cooler, moister regions may germinate more rapidly than those from other areas, giving them a long-term advantage in growth in cooler areas.

Bergin & Kimberley (1992) show that the germination of *P.hallii* was very poor for most seedlots (data not given). Burrows (1995) recorded *P.hallii* germination from Banks Peninsula at 3-15 months after seed trays were brought from the forest back to the glasshouse, with no subsequent germination after 15 months.

Bergin & Kimberley (1992) noted a number of characteristics of *P.totara* seed viability: seeds with full white endosperm were considered sound, green seed collected off trees were hollow even when the receptacle was ripe, and seed collected in late spring and summer had low viability.

2.4 TIMBER UTILISATION

2.4.1 Wood anatomy and chemistry

The anatomy and wood characteristics of the four *Podocarpus* species are discussed by Patel (1967) and presented by Meylan & Butterfield (1978). Without exception the wood of New Zealand gymnosperms have predominantly uniserate rays (Meylan & Butterfield 1978) and the four *Podocarpus* species have taxoid pits (Patel 1967). The four species can be distinguished on the basis of tracheid length, ray height, ray parenchyma walls, and growth rings and Patel (1967) uses these in an identification key using a minimum number of wood characteristics.

Patel (1967) also divides the New Zealand *Podocarpus* (as it stood then) into the

three groups proposed by De Laubenfels (1969, 1978) on the basis of wood characters. Kaeiser (1954) investigates the wood microstructure of 106 *Podocarpus* species in an attempt to determine if wood microstructure agreed with the taxonomic treatment of the genus at the time. Kaeiser (1954) found her results accorded with those of Bucholz & Gray (1948) in that the four present New Zealand *Podocarpus* species are in section *Eupodocarpus*, sub-section D.

The chemical constituents of the four species have been reviewed by Cambie (1976). All New Zealand *Podocarpaceae* contain bioflavenoids in the leaves (Cambie & James 1967). Insect moulting activity has been found in the wood and bark of *P.acutifolius* and *P.nivalis* (Russel & Fenemore 1970). *P.acutifolius*, *P.nivalis*, and *P.totara* all contain totarol, podototarin, and podocarpic acid whereas *P.hallii* only contains totarol and podocarpic acid (Cambie 1976). This lack of podototarin in *P.hallii* was investigated by Cambie, Simpson & Colebrook (1963) and their comparisons of the heartwood of *P.totara* and *P.hallii* lent support to the classification of *P.hallii* as a true species. The Great Britain DSIR (1945) reports that primer paint drying is retarded by the heartwood extractives of *P.totara*.

2.4.2 Timber properties and uses

P.totara is considered more viable as a timber species than *P.hallii* due to *P.hallii*'s smaller stature and tapered boles. *P.totara* is valued as a specialty timber on account of its excellent property of durability combined with lightness and ease of working. The heartwood is considered very durable for 25 years and has low shrinkage and moisture content figures (Clifton 1990). Although totara has high dimensional stability, it is neither very strong or very stiff. Heartwood is an even reddish-brown and the sapwood pale brown. The grain is straight and so it splits easily and it has a fine even texture which cuts smoothly across the grain (Clifton 1990).

Air seasoning is recommended (9 months for 25mm boards) rather than kiln drying which is uneven and can drive off the extractives which give lowland totara its durability (Hinds & Reid 1957). Further information on seasoning properties, preservative treatment, and mechanical properties are provided by Great Britain DSIR (1945), Hinds & Reid (1957), and Clifton (1990).

Heart-rot is common and veteran trees are usually hollow. Honeycomb-type decay of the heartwood is common in mature trees, especially in North Island, although this is non-active after seasoning and does not detract from durability. *P.totara* is

reported to be susceptible to attack by the common furniture beetle, *Ambeodontus* (Gt Britain DSIR 1945) but not to *Anobium* borer attack (Hinds & Reid 1957). Cunningham (1963, 1965) notes 13(11) species in 8(7) *Polyporaceae* genera and 12(13) species in 6(7) *Thelephoraceae* genera which attack *P.hallii* (*P.totara*). *Hymenochaete stratura* is specific to these two species.

The most predominant use of *P.totara* timber during this century has been for fence posts, although it was sought after for house piles and exterior woodwork. Its durability has caused it to be much employed for railway-sleepers, wharf-piles and telegraph-poles (Cockayne & Phillips Turner 1939). Clifton (1990) reports that from 1921, when records were first kept, until the mid-sixties production of *P.totara* sawn timber fluctuated between 20,000 and 40,000m^3 per annum - always less than *Dacrycarpus dacrydioides* and *Prumnopitys taxifolia* and only about 6% of *Dacrydium cupressinum* production. For the year ended 31/3/1988 only 680m^3 was cut, mostly from the King Country. Only select logs are sawn today, mainly for special purpose projects involving Maori carving.

2.4.3 Cultural values and uses

In northern New Zealand *Agathis australis* and *P.totara* were both held in high regard by Maori. Over the rest of the country, however, *P.totara* was indisputably the most revered tree in the forest. *P.totara* has a mythical origin assigned to it and is regarded as the principal member of the rakau rangatira - superior or lordly trees (Best 1977). Tradition made *P.totara* a direct descendant of Tane, through mumuhanga, the Gentle Noise of Air, who became its special presiding deity (Gordon 1944). Tuhoe Maori recognised two sexes for *P.totara*, the male tree termed karaka and the female kotukutuku (Best 1977).

Maori used *P.totara* to fashion canoes, the best trees coming from within the forest. Fern fronds were laid upon the stump as offerings even after Tane had removed himself (Gordon 1944). Best (1977) also records that Maori considered a *P.totara* split in felling as representing misfortune and that small hardwood wedges were used to split the tree. *P.totara* trees were planted to mark a special birth and old trees were treated as heirlooms with their own special names (Gordon 1944).

Other traditional uses of *P.totara* include using the heartwood for carving; the front of the chief's house always showed finely carved gable ends. Best (1977) discusses the use of the inner bark of *P.totara* being used for bark vessels for food and water. Batley (1956) describes mutilated *P.totara* from which bark was removed to

construct mutton bird containers or poha. The thick fibrous bark also made excellent thatching and the timber was used extensively in the construction of a fortified pa (Clifton 1990). Branchwood was used for adze handles and beaters (Cooper & Cambie 1991).

Crowe (1990) recounts the edibility of *P.nivalis* and *P.totara* berries (peduncle) although they are considered to be constipating. Maori men would climb *P.totara* trees and collect fruit by the basketfull and they would then be eaten raw. Brooker, Cambie & Cooper (1987, 1988) lists the medicinal uses of *P.totara*, as used by Maori, as: smoke of burning wood for skin complaints, venereal disease, and haemorrhoids; outer bark for splints in bone fracture; and a fever reducer made from an extract of the inner bark of *P.totara* and *Leptospermum scoparium*.

Early European explorers collected *P.totara*, among other principal trees, and three Wardian cases containing young plants arrived at Kew in good condition in 1838 (Cooper & Cambie 1991). Venerated as *P.totara* was by Maori, it was regarded with equal awe by pioneer European farmers for it was considered the perfect fencing timber (Clifton 1990). The extensive deforestation of New Zealand's lowland podocarp forests then began.

2.5 POPULATION DYNAMICS

2.5.1 Historical ecology

Pre-human history

The first appearance of the podocarps can be traced as far back as the lower Triassic (248 million years B.P.) with the identification of *Mataia podocarpoides* from Canterbury leaf material (Townrow 1967). Disaccate *Podocarpus* pollen has been found as early as the upper Triassic in the Mesozoic era circa 200 million years B.P. (Fleming 1975, Mildenhall 1980), with Podocarpaceae pollen becoming common in New Zealand fossil beds in the Cretaceous period 100 million years B.P. (Couper 1953).

Podocarpaceae species dominated pollen floras during the Cretaceous period when land bridges between early New Zealand and the other continents were broken although angiosperms were becoming more important in the fossil record (Fleming 1975).*Dacrycarpus* pollen was identified in the lower Eocene epoch circa 40 million

years B.P. (Mildenhall 1980) and the first lowland totara macrofossil was located in lower Miocene (24 million years B.P.) beds (Fleming 1975).

The pre-human history of New Zealand's vegetation has been determined by analysing the pollen record. Pollen of individual *Podocarpus* species is hard to distinguish and makes interpretation somewhat difficult. During the glacial maximum (22,000 to 14,000 years B.P.) the vegetation of central South Island was predominantly shrubland or grassland (Moar 1980, McGlone 1988). Podocarp - broadleaves were rare, with rimu and matai representing less than 1% of the pollen taxa (McGlone 1988). During the late glacial period (14,000 to 10,000 years B.P.) rimu and matai were dominant in the central North Island (McGlone & Topping 1977) due to forest recolonisation. There was no corresponding irruption of forest in the South Island (Moar 1971).

During the period 12,000 to 9,500 years B.P., the strong westerly circulation continued to dominate South Island and only sheltered areas could support forest. Temperatures continued to rise but precipitation was less than at present. McGlone (1988) suggests that the rising temperature may by increasing evapotranspiration have given the competitive advantage for close to 2,000 years to drought-tolerant podocarps such as lowland totara and matai. Nearly all of the trees predominant during the early part of the late glacial (matai, kahikatea, totara) are characteristic of fresh, nutrient-rich soils which were deposited in this period.

At circa 10,000 years B.P. (beginning of Holocene epoch) there was a substantial New Zealand-wide change in vegetation (McGlone 1988). Podocarps, broadleaved canopy and subcanopy trees became common. The first South Island forests were matai-kahikatea and totara-matai in the east and rimu in the west, with beech present in the uplands only (McGlone 1983a). In inland regions of northern South Island, matai, lowland totara, and Hall's totara became dominant elements in Holocene *Phyllocladus alpinus* forest, although they failed to completely replace this species (Moar 1971). Burrows et al (1993) discuss the vegetation history of the Arrowsmith Range, Canterbury, during the Aranuian (14,000-6,000 years B.P.). where Hall's totara and *Phyllocladus alpinus* were the dominant trees from 10,000-2,000 years B.P.

At 9,500 years B.P. only central Otago remained unforested. Forest was slow to colonise central Otago and only reached the dry areas 7,500 years B.P. (McGlone 1983a), hill forests of the region being predominantly matai-Hall's totara. By 9,500 B.P. the last remaining cool-climate species disappeared from the lowlands and

drier eastern areas were dominated by conifer-broadleaf forests (containing lowland totara, matai, and kahikatea) (McGlone 1988).

Much lowland totara wood was present on the Canterbury plains around 4,000 to 2,500 years ago, the inland basins supporting grasslands on young alluvium and accumulating loess (Molloy 1969). Pre-Polynesian Canterbury vegetation is discussed by Molloy et al (1963) and Molloy (1969) and lowland totara appears to have been an important component both on the upper plains and on lower hill country.

Deforestation through natural fires began approximately 2,500 years ago (McGlone 1983a) and devastated forests and shrublands in central Otago. There are indications that some forest was burnt at the same time in southern Canterbury (McGlone 1988).

Polynesian and European deforestation

Nicholls (1980) recounts that 1000 years ago forest covered three-quarters of New Zealand; 850 years later Polynesians had destroyed 30% of it; in the last 150 years Europeans have destroyed a further 40%, with the greatest proportionate loss being of flat lowland areas. Blaschke et al (1981) estimate the amount of lowland podocarp and podocarp-hardwood forest presently remaining in New Zealand to be 3.3% of the land surface. The distribution of indigenous forests in both 1880 and 1976 is graphically demonstrated by Saunders (1983). Godley (1975) shows the distribution of indigenous forests in both North and South Island, showing lowland totara to be of lesser extent than more merchantable species such as rimu.

Polynesian burning began in coastal areas c. 950AD (Molloy 1969) with the most widespread clearance occurring from 1150-1350AD (Molloy et al 1963, McGlone 1983b). By 1650AD most lowland forest vulnerable to fire had been burnt, with Europeans clearing the remainder for agriculture and timber (McGlone 1983a). Burrows et al (1993) document fires removing the remaining Hall's totara forests of the Arrowsmith Range area in circa. 1850 and 620 years B.P. Charred surface logs of Hall's totara found in the central Otago area are from fires within the last 150 years (Wells 1968, 1972).

Esler (1978) documents the severe reduction in Manawatu regions natural vegetation since human settlement which is assumed to have been almost totally forested. Totara/matai forest would have been a significant forest type of the area

in pre-human times. Only 1.9% of the region has predominantly indigenous vegetation remaining from the original 312,300 hectares.

Banks Peninsula was also more or less continuously forested in pre-human times (see QEII National trust 1987, Wilson 1992). Presently the old growth forest cover is less than 1% of its pre-human extent and about 1.5% of its extent 150 years ago (Johnston 1969, Wilson 1992). These fragments of old growth forest represent the possible original forest type - that of totara, matai, and kahikatea, with Hall's totara on land above 500m. The present day distribution of forest and scrub in Canterbury is presented by Burrows (1969).

McSweeney (1982) estimates the amount of *P.totara* var. *waihoensis* -matai flood plain forests of south Westland to be circa 600 hectares from a possible 43,000 hectares, a reduction of around 99%.

2.5.2 Communities

Complementary classifications of the indigenous forests of the North Island (Nicholls 1976) and South Island (McKelvey 1984) provide the basis for the following community descriptions (for condensed national classification see Nicholls & Herbert 1986). Nicholls (1976) recognised 18 forest classes in the North Island (including 4 modified classes) of which 10 of the unmodified classes occur in the South Island (McKelvey 1984). Hall's totara is the most ubiquitous of the *Podocarpus* species, occurring in a wide range of forest classes (from kauri through rimu to beech) at all altitudes. Lowland totara only occurs in 4 forest classes. Forest classes containing totara and Hall's totara are further discussed by Norton et al (1988).

Lowland totara occurs in the following classes:

Class B - kauri-softwoods-hardwoods
I - rimu-general hardwoods-beech
L - softwoods
M - rimu-matai-hardwoods

In most communities lowland totara is a tall tree usually co-dominant with associated Podocarpaceae species. Only in association with kauri, rimu or kahikatea is lowland totara commonly sub-dominant. Class L (softwoods) consists of four main types where lowland totara is dominant:

• Kaikawaka/totara with some silver pine and sometimes matai. Only a few hundred hectares remain near west Taupo as small pockets on terraces that have been drained by incising streams and on swampy level terrain where it has co-existed in an intricate mosaic with the bog pine/mountain toatoa type (McKelvey 1963). This forest type was not encountered in the present study due to its restricted distribution.

• Kahikatea/totara (Wardle 1974, 1977). Wardle (1974) discusses the establishment of kahikatea on alluvial terraces in south Westland and states that thickets of *Coprosma propinqua* and *P.totara* var. *waihoensis* provide shelter for kahikatea seedlings, with totara being more dominant on dry, stony ground. The presence of totara on shingle ground in Westland is also noted by Foweraker (1929). Recent alluvial soils characterise the presence of totara/kahikatea/matai forest; on stonier and better drained soils kahikatea is equalled or exceeded in abundance by the other podocarps (Wardle 1974). As podsolization and gleying leads to decreased soil fertility, rimu gradually replaces kahikatea or, on better drained sites near the mountains, lowland totara. This forest type appears to intergrade with the following, depending upon soil type and drainage regime.

• Totara/matai. This forest association is recognised by Morton, Ogden & Hughes (1984) and McSweeney (1982) to be of greatly reduced extent and one of the rarest forest types containing mature dominant lowland totara. Two areas in New Zealand with this type are at Whirinaki State Forest Park and in south Westland (*P.totara* var. *waihoensis* Wardle 1972). Only about 700 hectares remain (McSweeney 1982, Morton et al 1984). Druce (1966) and Duguid & Druce (1966) describe secondary totara-titoki-matai forest remnants from the coastal Manawatu. Norton (1996) describes totara/matai forest on a Southland dune system at Otatara. Soil is described as old sand dunes overlying stony alluvium. Totara/matai forest was once common on river alluvium of the Manawatu (Ravine 1995). Several examples of this forest type were encountered in the present study. Species composition ranges from almost pure matai (see Plate 4) to totara/matai, to totara/matai/kahikatea.

• Dense mixed podocarps throughout (McKelvey 1963, 1973, Nicholls 1976, Wardle 1977). Lowland totara occurs in association with rimu, miro, matai and kahikatea and can occur as a continuous canopy above tawa with between 50 and 90 podocarp trees per hectare (Beveridge 1983). In these associations mature totara trees have a somewhat clumped distribution and regeneration is absent under the

canopy or in light gaps. This forest type is most common in North Island and eastern South Island colluvial slopes. In the present study, dense mixed podocarps on colluvial slopes were encountered in Blue Duck Scenic Reserve and Peraki Saddle Scenic Reserve (Plate 7).

2.5.3 Regeneration ecology

The literature concerning podocarp population dynamics and regeneration is critically reviewed by Morton et al (1984), Norton, Herbert & Beveridge (1988), and Ogden & Stewart (1996). The establishment of lowland totara in the wild has received little attention compared to other podocarp species such as rimu (e.g. requirements for germination, establishment, and growth to maturity in the forest environment). Further studies of these areas are presented in this chapter and will help in the elucidation of lowland totara population dynamics.

The terrace rimu forests of Westland exhibit a mosaic pattern of even-aged stands (see Norton et al 1988). Disturbance is seen as a major factor in the regeneration of these stands and for this reason seedlings and saplings of the canopy dominants are not expected to be present under a closed podocarp canopy. In a general discussion on conifer regeneration in New Zealand, Ogden (1985) argues that a "gap-phase" or "mosaic" regeneration model is most appropriate for New Zealands canopy conifers. Ogden (1985) sees the regeneration of New Zealand conifers as resulting from both small and large-scale disturbance events, the interaction between the two often complicating interpretation of forest dynamics.

Windthrow has been proposed as one mechanism initiating podocarp regeneration in dense lowland podocarp forest (Shaw 1983, Ogden 1985) and is seen on scales appropriate for these podocarp forests. Regeneration is rare under a dense podocarp canopy but does occur beneath a gradually opening hardwood canopy (Beveridge 1973a). A sequential canopy collapse theory is proposed by Lusk (1989) for dense podocarp forest: elevated light levels due to canopy collapse allows the more light demanding species to enter. As the canopy re-closes species stop entering depending upon their shade tolerance. Periodic large scale disturbance re-initiates the regeneration of dense podocarps.

Lowland totara has long been considered a light demanding species (e.g. Cameron 1960a, McKelvey 1963) with a pioneer strategy colonising infertile or recently disturbed sites, perhaps under a nurse crop (e.g. Greenwood 1949, Beveridge 1983). There is strong evidence that lowland totara is unable to regenerate beneath a

closed canopy or even in small gaps within the canopy. Its regeneration appears most vigorous in large windthrow gaps, forest margins or in open scrub and grassland (i.e. in high light or disturbed areas). If lowland totara is a light demanding species, canopy gaps would have to be very large to allow enough light to enter for totara to regenerate.

While a large time scale of establishment is shown by other podocarps (Katz 1980b, Lusk 1989) limited age data exist for lowland totara. In central North Island dense podocarp stands, the present mature lowland totara trees are too old to have been initiated by Polynesian burning and are not old enough to be the first generation after the Taupo eruption (Morton et al 1984). However, the establishment of dense pole stands containing large proportions of totara has been noted on abandoned Maori cultivation sites where a broad-leaved nurse crop under which podocarp species may establish develops 40-60 years following abandonment (Cameron 1960a). Burke (1974) states that establishment of lowland totara and Hall's totara resumed within 25 years of the 1886 Tarawera eruption.

In a recent study on podocarp seedling growth rates under different light regimes Ebbett & Ogden (1998) elucidate seedling strategies. Lowland totara is shown to have high seedling growth rates in elevated light levels such as those found under catastrophic disturbance regimes which destroy the canopy. Matai is a consistent grower, slowly attaining the canopy through persistence and shade tolerance. Miro is intermediate in shade tolerance and captures sites such as canopy gaps created by medium-scale disturbance events such as wind-throw.

Environmental conditions, particularly drainage, may dictate which species dominates the first cohort following disturbance, with totara on drier sites and rimu on wet (Ogden 1985). Podocarp species give a shallow mor-type acid litter which forms a poor dry seedbed, hence mature trees may effect regeneration in the vicinity (Cameron 1955). The sequence of regeneration to totara/matai and totara/kahikatea forest on the alluvial flood plains and terraces of south Westland and the role of silt deposition is discussed by McSweeney (1983), Wardle (1974), and Foweraker (1929).

2.5.4 Future management

The small areas of reserves and the failure of *P.totara* to regenerate under its own canopy raises the question of the future viability of these stands and the need for interventionist management. If high light levels and major disturbance events are

required to initiate *P.totara* stands, management and conservation goals may need modification.

2.5.5 Cultivation and restoration

Endemic New Zealand tree species are enjoying an increase in popularity for garden use. Metcalf (1991) discusses the use of *Podocarpus* species in the home landscape environment; *P.totara* for specimen trees, *P.totara* cultivar "Aureus" for coloured foliage and indoor containers, and *P.acutifolius*, *P.nivalis*, *P.totara*, and *P.totara* cultivar "Aureus" for hedges and shelter purposes. The suitability of *P.totara* and *P.hallii* for soil conservation purposes (i.e. wind and sheet erosion prevention) is discussed by Pollock (1986).

Due to the greatly diminished extent of *P.totara* dominated forest many workers have concentrated upon the artificial cultivation of *P.totara* to enable rapid reforestation of denuded areas.

The performance of planted *P.totara* on the basis of Forest Research Institute trials is discussed by James & Griffiths (no date), Pardy (1983a, 1983b), Beveridge, Bergin & Pardy (1987), and Bergin & Pardy (1990). Beveridge et al (1987) state that *P.totara* is easily established but can be coarsely branched partly due to frost and insect damage.*P.totara* survival rates of 60-80% have been recorded for 20-50 years old plantations where shelter was provided and competing vegetation removed from around seedlings (FRI 1989). *P.totara* is considered one of the fastest growing conifers in a plantation situation with a height of 17m and diameter of 61cm being reached after 60 years (FRI 1989) - a height similar to, and a diameter greater than, *Dacrycarpus dacrydioides* and *Agathis australis*.

With an increasing awareness of the value of forest remnants, and of the amount of impact that has occurred in New Zealand since human settlement, there has been a growing interest in attempting to restore our native forests. The large body of planting trials conducted by the Forest Research Institute has helped in providing information on how to conduct restoration projects in either cut-over or on bare land. Guidelines for the restoration of native species and their use in plantations have been prepared by the FRI (e.g. Beveridge et al 1987, Bergin, Pardy & Beveridge 1988) although little information exists concerning the artificial establishment of natural forest associations. One study in Canterbury concerns the restoration of *P.totara* / *Prumnopitys taxifolia* dominated forests on Banks Peninsula (Norton 1992), a once prevalent forest type of the region.

2.6 SUMMARY AND FURTHER RESEARCH

Literature concerning *P.totara* is reviewed above, showing several areas where further research undertaken in the present study will help to elucidate the ecology of this species:

• Present day distribution and niche requirements of lowland totara are not well documented in the literature. A study of totara's present distribution would elucidate the ecological preferences of this species and determine which areas are suitable for the future regeneration of this species. Data on current distribution, and niche requirements are presented in Chapter Four.

• In-depth studies of lowland totara dominated stands are lacking from the literature although forest types are well documented. Questions concerning species coexistence and forest associations are addressed in Chapter Six.

• Seedling growth rates and establishment of lowland totara is poorly understood although a requirement for high light is apparent. This high light requirement indicates regeneration after catastrophic disturbance although this is poorly documented in the literature. Further studies on seedling distribution, establishment, and disturbance regimes are presented in Chapters Five and Seven.

• Stand structure and development through time is poorly understood. Chapter Six details stand spatial structure, species associations, and canopy development through time. An understanding of the development of totara dominated stands will help in the prediction of future stand structure and the classification of the forest type.

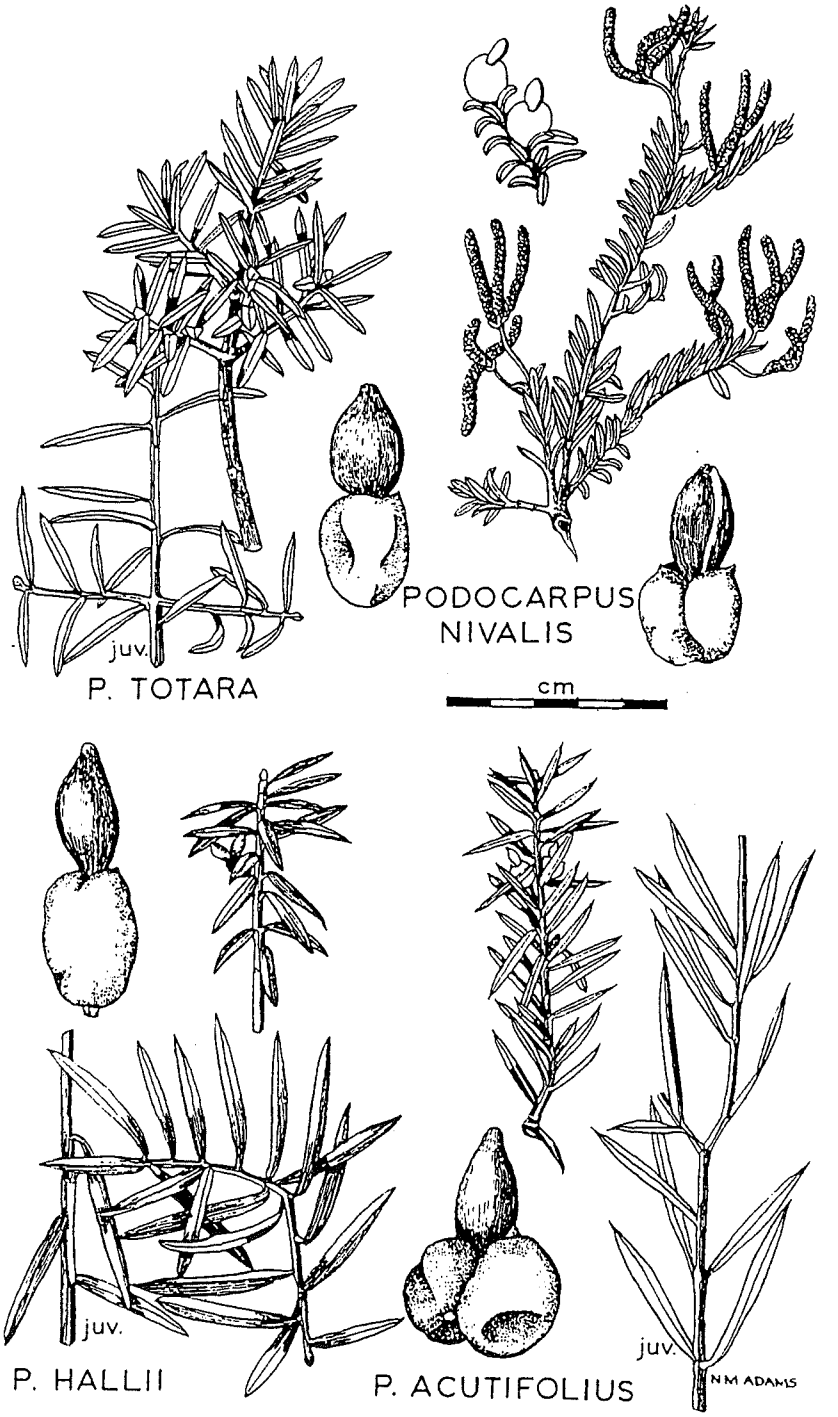
• On the basis of the previous investigations, an overview of the ecology of lowland totara is presented in Chapter Ten. With an understanding of the ecology of lowland totara, one can then address the survival of this species in the future.

• Forest fragmentation and its effects has received considerable attention in recent literature. A review of fragmentation is presented in Chapter Eleven as well as an example of fragmentation (Banks Peninsula). Data on forest reduction is presented.

• Chapter Twelve presents an integrated landscape plan to provide for the regeneration of lowland totara in the future based on regeneration requirements. A

questionnaire of landowner attitudes is presented as well as options for landowners to provide for the future regeneration of lowland totara. Other landuse issues such as soil protection are discussed.

Figure 2.1 Line drawings of the New Zealand *Podocarpus* species (from Poole & Adams 1986).



CHAPTER THREE
DATA COLLECTION & TREE AGEING

3.1 INTRODUCTION

This chapter details study site selection, data collection, and tree ageing methodologies. Lowland totara was the primary study species, although at some sites hybrids with hall's totara occur. Study sites were selected from around the northern half of South Island, ensuring adequate coverage of the full range of environmental conditions such as climate, geographical location, and landform position that lowland totara experiences.

Many of the analyses performed in this thesis rely on absolute tree ages. For this reason, tree ageing methodology is critically examined in this chapter and tree age error estimates are given. As it was not logistically possible to age all trees present at a site, details of the use of regressions for determining age from tree size are outlined.

3.2 STUDY SITES

3.2.1 Introduction and objectives

The objectives for selecting study sites are:

• To ensure adequate coverage of geographical location and climate in the northern half of South Island. To fulfill this objective, at least two study sites each were selected from Westland, Canterbury, and Northwest Nelson.

• To ensure adequate coverage of a range of landforms and soils. To fulfill this objective, at least two study sites each were selected from dune systems, alluvial terraces, alluvial fans, and colluvial slopes.

• Ensure adequate coverage of all lowland totara forest types and development status. To fulfill this objective, at least two study sites each were selected that

contained young/colonising, developing, and mature stands. An aditional senescent stand was selected.

Accessability was a secondary factor in site selection. Selecting study sites was relatively straight forward as many of the remaining totara dominated stands of significance are in some form of protection. All study sites are either Scenic Reserves or privately covenanted stands. Department of Conservation permits and landowner permission were obtained for visiting all study sites prior to fieldwork. Permission to core trees and collect herbarium specimens was also obtained.

3.2.2 Methods

Stand development status is classified as young/colonising, developing, mature, or senescent, based on tree age, canopy structure, and the presence of seedlings and saplings.

• Young/colonising stands were classified by the absence of emergent trees, small tree diameters, and abundant seedlings. Young/colonising stands generally occur on dune formations or alluvial terraces i.e. recently available colonisation surfaces.

• Developing stands were classified on the basis of having either a relatively open canopy or several emergent podocarps. Seedlings and saplings are common and a wide range of tree diameters are present.

• Mature stands were classified on the basis of having a more or less continuous canopy of evenly sized large podocarps with few seedlings or saplings.

• Senescent stands were classified on the basis of having several fallen dead giants (circa 150cm diameter). The canopy consists of large diameter emergents over a mature subcanopy of broadleaves. Seedlings are uncommon.

3.2.3 The study sites

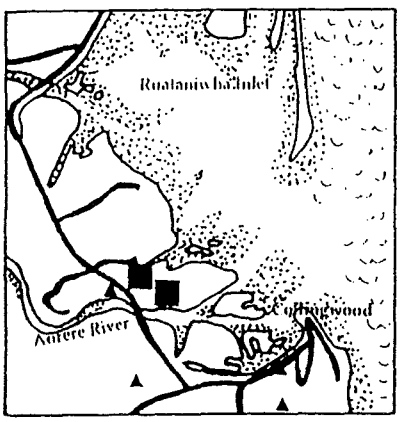
Study sites were selected from a variety of climate zones around the northern half of South Island (Nelson/Marlborough, Canterbury, Westland; Fig. 3.1.). Topographical map references for the ten study sites appear in Table 3.1 and geological map references in Appendix Two. Table 3.2 outlines the ten study sites in terms of stand development status, forest type, and ecological district. Forest type ranges from pure totara, matai, totara/matai, totara/matai/kahikatea, to

dense mixed podocarps. The following references contain further information on several of the Reserves selected for study sites; Kaikoura (Williams 1982), Canterbury (Kelly 1972), Nikau Reserve (Loh 1981).

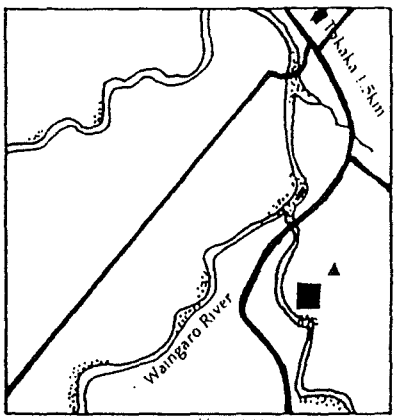
Table 3.1 Topographical map references for the ten study sites. [1]D.S.I.R. (various). 'New Zealand topographical map 1:63360.' Government Printer, Wellington. [2]D.S.I.R. (various). 'New Zealand topographical map 1:50000.' Government Printer, Wellington.

	NZMS1 1:63360[1]		NZMS260 1:50000[2]	
STUDY SITE	Sheet	Grid location	Sheet	Grid location
Mananui S.R.	50	475500	J33	382232
Nikau S.R.	37	842247	K30	717944
Dennistoun Bush S.R.	91	770114	J37	684989
Okuti Valley S.R.	94	173252	N36	965137
Peraki Saddle S.R.	94	195205	N37	986094
Puhi Puhi S.R.	49	018072	P31	709815
Blue Duck S.R.	42	065115	P31	750852
Coke Covenant	3	075032	M25	814592
Payne's Ford S.R.	8	209766	N26	941351
Price's Valley Covenant	94	275070	M36	871155

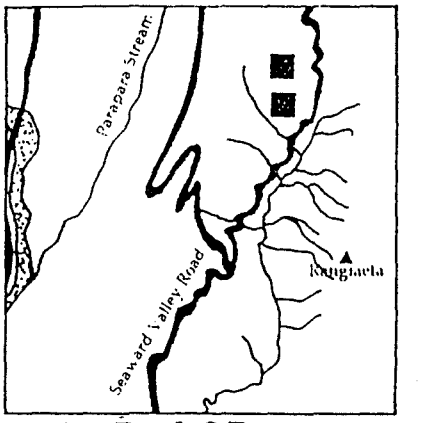
Figure 3.1 Location of ten study sites and sixteen study plots, South Island, NZ.



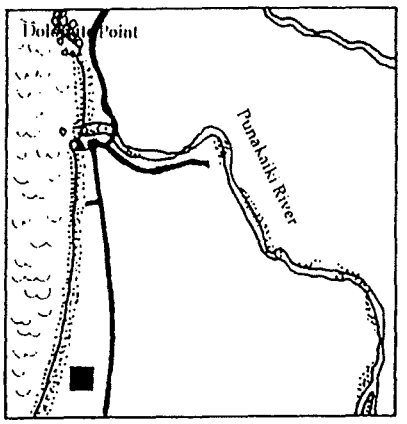
3. Coke Covenant



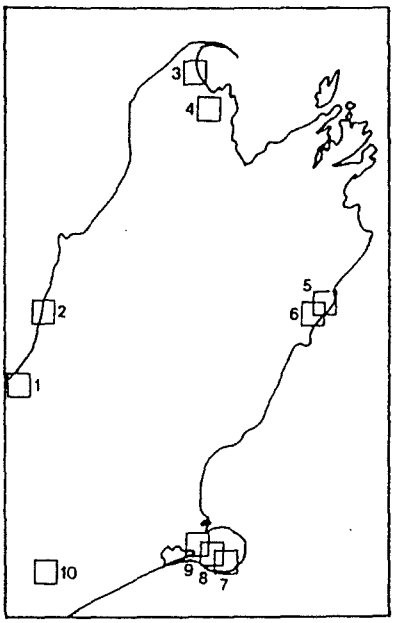
4. Payne's Ford S.R.

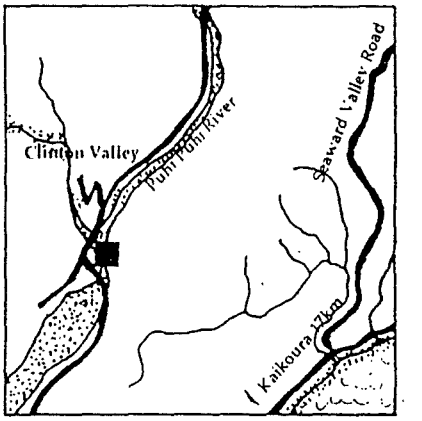


5. Blue Duck S.R.

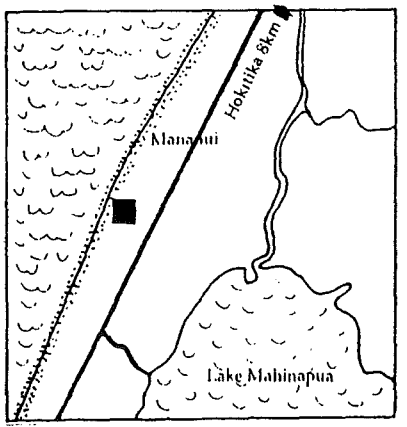


2. Nikau S.R.

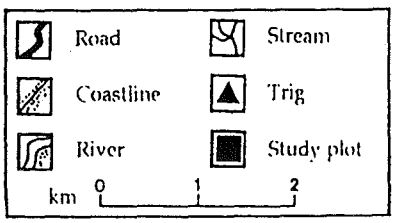


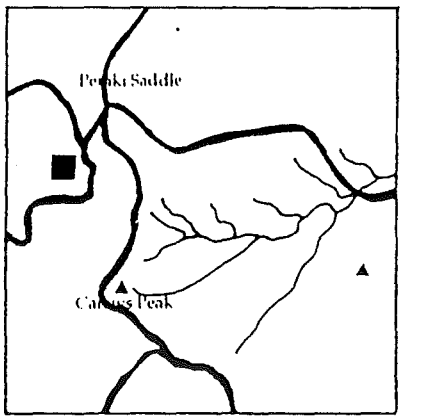


6. Puhi Puhi S.R.

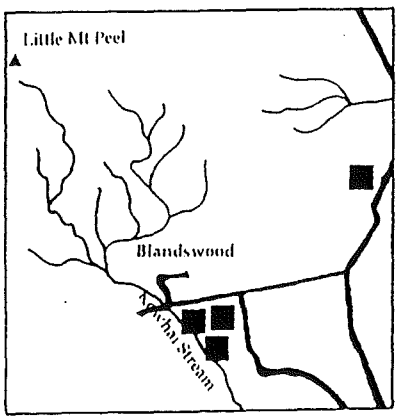


1. Mananui Bush S.R.

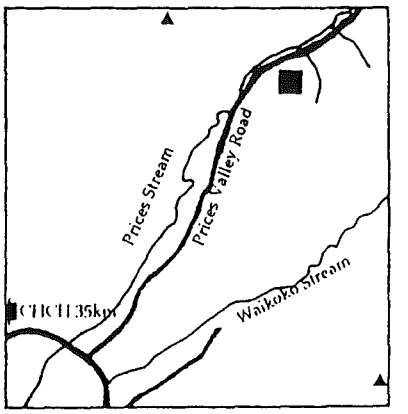




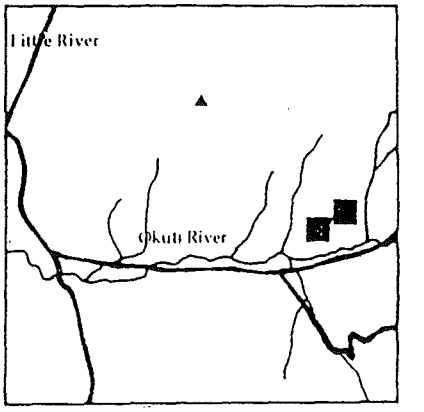
7. Peraki Saddle S.R.



10. Dennistoun Bush S.R.



9. Price's Valley Covenant



8. Okuti Valley S.R.

Table 3.2 Development status, forest type, and ecological district of the ten main study sites.

STUDY SITE (conservation status and location)	DEVELOPMENT STATUS	FOREST TYPE	ECOLOGICAL DISTRICT
Nikau Scenic Reserve Punakaiki, WESTLAND	young/ colonising	dense mixed podocarps	Westland
Mananui Scenic Reserve Hokitika, WESTLAND	young/ colonising	totara/dense mixed	Westland
Puhi Puhi Scenic Reserve Kaikoura, MARLBOROUGH	young/ colonising	matai/scattered totara	N/w Nelson
Okuti Valley Scenic Reserve Banks Pen., CANTERBURY	developing	totara/matai	Canterbury
Coke QEII Covenant Collingwood, NELSON	developing	totara/matai	N/w Nelson
Payne's Ford Scenic Reserve Takaka, NELSON	developing	pure totara	N/w Nelson
Prices Valley QEII Covenant Banks Pen., CANTERBURY	mature	matai/scattered totara	Canterbury
Blue Duck Scenic Reserve Kaikoura, MARLBOROUGH	mature	dense mixed podocarps	N/w Nelson
Peraki Saddle Scenic Reserve Banks Pen., CANTERBURY	mature	totara/matai	Canterbury
Denn. Bush Scenic Reserve Peel Forest Park, CANT.	mature and senescent	kahik/totara & tot/mat/kah	Canterbury

3.3 DATA COLLECTION

3.3.1 Introduction

Once the study sites were selected, the data collection methodology described below was applied. Data were collected in the field in the form of plot maps, enabling further analysis of tree locations. Tree ages were determined from ring counts and regressions. The eror involved in tree ageing was investigated.

3.3.2 Plot map methods

Once the ten main study sites were selected, study plots were delineated for the purposes of data collection. Where remnants were small, only one study plot was surveyed. Larger stands with a variety of forest types contained two plots e.g. at Dennistoun Bush, Okuti Valley, and Blue Duck. Data from Denn Huge was collected in three adjacent plots but analysed together due to the small numbers of totara individuals.

Figure 3.2 shows the size and stand development status of the study plots. While plot size varies from 0.02ha to 0.5ha, all boundaries were subjectively chosen so as to contain the majority of totara trees in a particular area (i.e. patch). For the purpose of plot delineation, the minimum number of totara adults present in a study plot was set at six, except for the almost pure matai stands in which totara was rare. Plots were located as far away from remnant edges as possible to eliminate the possibility of sampling "edge forest".

Vegetation details at each site were recorded on a plot map using the rapid mapping technique developed by Ebbett (1992). Study plots were divided into 10m wide strips for the purpose of data collection. Each 10m strip was delineated with baseline measuring tapes, adjusted at 10m intervals to account for minor topographical variation. Data were then collected along each 10m wide strip (i.e. subplot) and subsequently analysed together as one plot. Slope was measured along each transect tape at 10m intervals to produce plot contour maps.

The distance to the centre of each individual tree was recorded at 90^0 to the baseline tapes using a previously calibrated electronic distance meter (SONIN 2000®). This recording proceedure gives an x/y co-ordinate for each individual (distance up and across). Species (seedling, sapling, adult), status (alive, fallen dead, standing dead), canopy position (understorey, canopy, emergent), DBH (diameter at breast height, 120cm), height, and core number was recorded for each individual. Tree height was estimated by comparison with a field worker of known height. Canopy position was subjectively allocated.

All podocarps over 50cm high and all angiosperms over 10cm DBH were recorded. Only seedlings over 50cm in height were recorded as those under this height are likely to be ephemeral. Tree ferns were excluded. The following size definitions are used consistantly throughout this thesis:

- seedling < 5cm DBH and >50cm high

• sapling 5 - 9.9cm DBH
• adult ≥10cm DBH

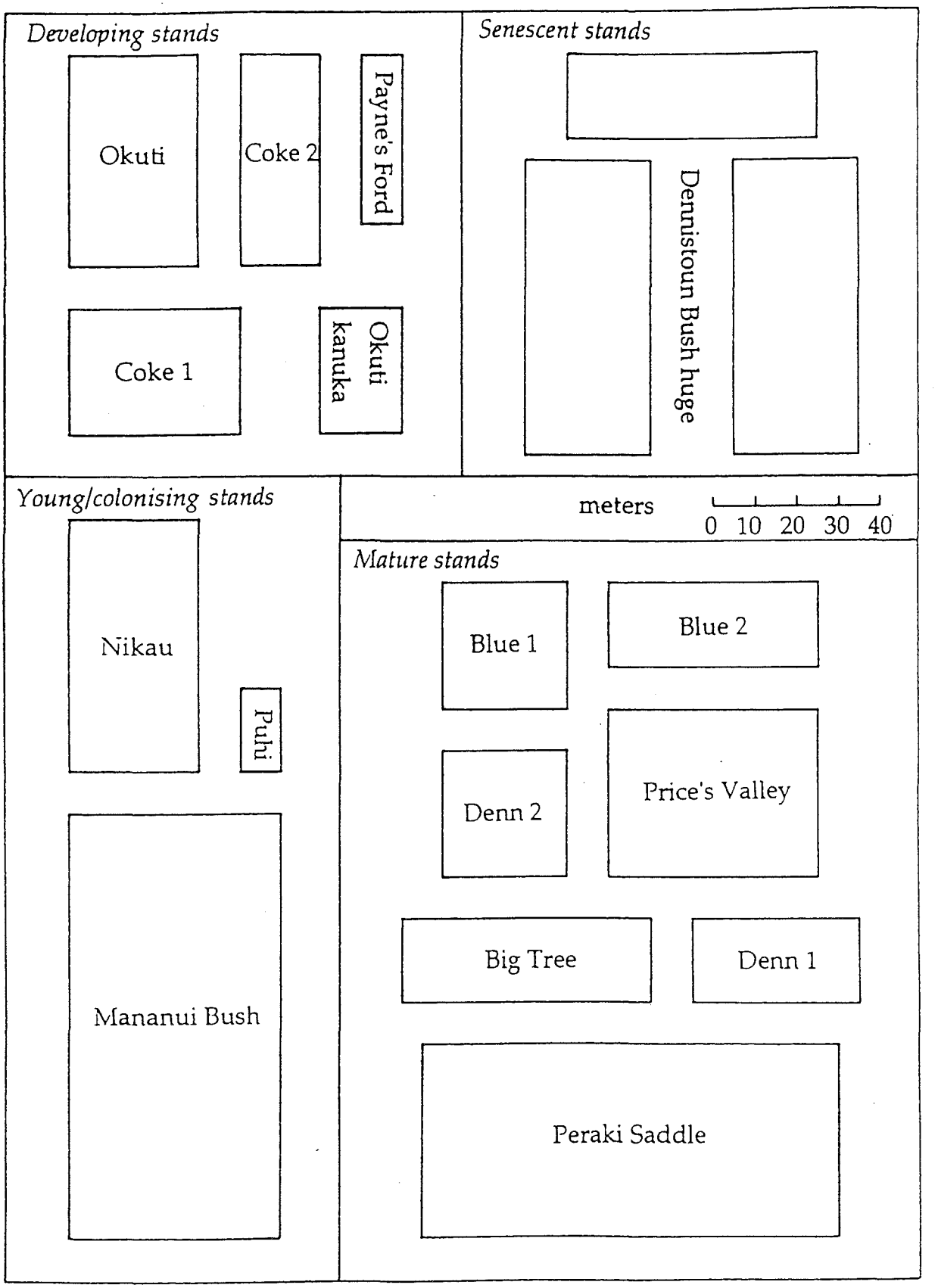
Additional information was recorded for the following:
• Fallen dead trees: Species (if possible), length, DBH, direction of fall, condition of base (snapped, uprooted).
• Standing dead trees: Species (if possible), height, DBH. Very decomposed stumps were excluded.
• Multiple stemmed trees: If the stem branched below 1.2m then each stem was measured at 1.2m and the tree recorded as being multi-stemmed. Basal area figures were calculated using the largest stem value.
• Epiphytes: DBH tape was either passed under these or DBH without epiphytes estimated.

A species list of the most common plants in and around plots was compiled and voucher herbarium specimens collected (see Appendix One). The presence of invasive weed species was also noted. Vertical structure and canopy composition of the stand was recorded to give data for profile diagrams. Half of the plots had additional information recorded on seedling position (level, elevated, depressed) and overhead cover (parent, gymnosperm, angiosperm).

3.3.3 Summary of data collection

Data were obtained from a total of 2.85 hectares (7 acres) of lowland totara dominated forest (16 plots in 10 study sites) and represents approximately nine weeks in the field with two people.

Figure 3.2 Size and development status of the study plots.



3.4 TREE AGEING

3.4.1 Introduction

The potential applications of dendrochronological studies in New Zealand have been reviewed by Norton & Ogden (1987). These techniques, based on increment cores or cross-sections, can be used to establish chronologies, age trees, or date events. Norton & Ogden (1987) list other applications of dendrochronological techniques including climate reconstruction, dating archaeological artefacts, and detecting atmospheric pollution, seed production, and insect epidemics. Lowland totara has long been considered to offer potential in tree-ring analysis (Bell & Bell 1958, Cameron 1960b) particularly due to its importance to Maori and the use of lowland totara for dating archaeological sites (Batley 1956, Bell 1958).

However, problems with using *Podocarpus* tree-rings to develop chronologies have also been noted. Annual growth rings and good circuit uniformity have been reported for Hall's totara (Wells 1968, 1972) although missing rings were also noted. Severe wedging and lobate growth has been noted in lowland totara and Hall's totara (Dunwiddie 1979). Hinds & Reid (1957) consider the growth rings of lowland totara to be relatively poorly defined. The problematic factors of false rings and lack of circuit uniformity make lowland totara ring patterns difficult to read and several authors suggest that work with totara should proceed by use of complete cross-sections rather than increment cores (Bell 1958, Bell & Bell 1958, Norton, Palmer & Ogden 1987). However, after observation of the cores collected in the present study, annual growth rings were assumed for the podocarps cored.

Absolute tree age dating using ring counts has been used extensively for other members of the Podocarpaceae (e.g. Katz 1980b, Herbert 1980) but rarely with *Podocarpus* species. Bell (1958) reports a 91cm diameter at breast height (DBH) lowland totara tree being aged at 256 years and an 18cm DBH tree at 350 years. Ebbett (1992) showed a 50 year age range for 30cm DBH lowland totara trees. Lloyd (1960) suggests that a more accurate age may be determined by grouping sets of rings which are separated by a wider band of spring wood than occurs within the set itself. Direct age determinations of trees by growth ring counts have provided information concerning abandoned cultivations (Ebbett 1992) and other Maori activities (Batley 1956).

To eliminate some of the error involved in absolute tree aging from cores, two cores per tree were used in the present study whenever possible. An estimate of error is also tabulated and compared to other studies. Growth rate data used in this study represents ten year mean ring widths to show general trends. No attempt has been made in the present study to crossdate podocarp growth rings or to correlate these with climatological data.

3.4.2 Tree coring methods

Tree cores were collected using corers from as many podocarps as was practical at a site (see Plate 3). Where only one core was taken, extraction was along the longest radius to minimise errors due to missing rings. All wounds were treated with a fungicide to prevent infection after coring. Table 3.3 shows the number of cores collected from all study sites.

The percentage of podocarps cored in each plot ranges from 12 - 88% (mean=54%), the percent of totara trees cored in each plot ranges from 12 - 100% (mean=66%). In most cases two cores per tree were collected to reduce the error associated with determining tree ages. Both small and large trees (less than 10cm DBH and greater than 70cm DBH) are under-represented due to the difficulty of coring. The ages of these trees were determined using regression equations.

No cores were taken from Nikau Scenic Reserve due to the wai tapu status of the area, or Prices Valley and Peraki Saddle due to the large size of the podocarps. Complete cross sections were obtained from seven fallen dead kanuka trees in Okuti Valley Scenic Reserve to determine the age of this possible nurse crop and past disturbance events.

Table 3.3 Number of tree cores collected (all plots).

SPECIES	Number of trees (saplings & adults)	Trees cored Number	(%)	Total number of cores collected
TOTARA	231	137	(59)	203
MATAI	78	24	(31)	53
KAHIKATEA	46	32	(70)	55
MIRO	4	3	(75)	6
KANUKA	25	7	(28)	6 trunk sections

3.4.3 Tree ageing methods

Cores were air-dried, mounted, and then sanded with progressively finer grades of sandpaper until rings were clearly visible. Ring counts were then made under a 10x binocular microscope. If the core did not pass through the centre of the tree the curvature of the inner rings was used to indicate the location of the centre by tracing the arcs of the inner rings and then fitting circles to them using a compass (Norton et al 1987). The number of rings in the missing radius was then determined by dividing the missing radius by the width of the first twenty countable rings, on the assumption that ring width will be somewhat similar due to the close proximity of the innermost rings to the centre of the core.

The total error in age estimates based on cores is due to the combination of errors associated with missing rings and estimating the age of the missing radius (Norton et al 1987, Duncan 1989). Tree age was determined as a mean of the core counts, weighted for the reliability of each core (missing radius / core length x 100 = % reliability). More emphasis is placed on the more reliable core by weighting the age estimates on the basis of reliability using the following standard mathematical equation;

$$\frac{(\%\ \text{reliability x age core 1}) + (\%\ \text{reliability x age core 2})}{(\%\ \text{reliability core 1} + \%\ \text{reliability core 2})}$$

An adjustment value for time to reach coring height (1.2m) was then added to determine absolute tree age (Table 3.4). Values for seedling height growth represent the mean of three replicates in 30% of full sunlight in the forest environment (Ebbett 1992). Herbert (1980) determines a period of 22 years for rimu to attain stump height (1.2m) and Bellingham (1982) applies this value to matai.

Table 3.4 Podocarp adjustment values for years to reach coring height (data from Ebbett 1992).

PODOCARP SPECIES	Height growth (cm per annum)	Core Height	Years to Add (adjustment value)
miro	17.4	120cm	7
matai	4.5	120cm	27
rimu	7.6	120cm	16
totara	13.3	120cm	9
kahikatea	8.2	120cm	15

3.4.4 Tree age error estimate

Many of the results in the present study rely on the interpretation of tree age data and annual growth ring counts. Age estimates need to be as accurate as possible to determine age-class frequency distributions and hence infer stand dynamics. An assessment of the degree of error involved in tree aging is therefore important.

Trees which had two or more cores collected were used in the determination of an absolute tree age error estimate. For each tree the percentage difference between minimum and maximum age estimate from the mean age estimate was calculated using the method described by Rogers (1995). Mean percent difference in age was then calculated and used to determine the total tree age error for each species. Table 3.5 shows the results of this error estimation. Error values for each of the main species is given for both 250 and 150 year old trees; for lowland totara this error is 13 and 22 years respectively. There appears to be no correlation in degree of error between DBH and age range.

Table 3.5 Absolute tree age error estimate.

Species	Number	% min.dif.	% max.dif	Mean %	250 years	150 years
totara	53	9.3 ± 8.4	8.0 ± 6.5	8.65	±22	±13
matai	19	8.6 ± 7.3	7.5 ± 5.9	8.05	±20	±12
kahikatea	21	12.1 ± 13.1	9.7 ± 9.2	10.9	±27	±16

Other studies have employed similar methods for estimating percent difference from the minimum and maximum age estimate to determine an overall tree age error estimate. Table 3.6 outlines tree age error estimates in this and other studies.

Error estimates derived in the present study are generally less than those found by other authors. No other data was found for lowland totara age error estimates. Matai's age estimate error range from 20 to 79 years, although larger sample sizes show a lesser error. Kahikatea's age estimate error appears to be circa 26 years. Miro and rimu show higher error in age estimates from ring counts (circa 42 years), although again sample sizes are small.

Table 3.6 Comparison of tree age error estimates (± years in 250 year old trees) for podocarp species in this and other studies.

SPECIES	N	Tree age error estimate (± years)
totara	53	22 (present study)
matai	19	20 (present study)
	4	c.79 (Bellingham 1982)
	18	c.25 (Norton et al 1987)
kahikatea	21	27 (present study)
	12	c.25 (Duncan 1989)
miro	4	42 (Rogers 1995)
rimu	4	42 (Rogers 1995)

Results from the present study indicate that 250 year old trees will have an age estimate error of 20 - 27 years (Table 3.5). Younger trees (circa 150 years old) show considerably less error when determining absolute age from ring counts (12 - 16 years). Comparison with other studies (Table 3.6) indicates that a minimum error of approximately 25 years is found for matai and kahikatea. All aged stands in the present study, except Dennistoun Bush, are ≤150 years old and so have less error involved in the absolute age estimates. Dennistoun Bush stands are a maximum of circa 230 - 320 years old.

On the basis of these error estimates, age classes used in further analysis will be 30 years. This age class size is considered to be small enough to reduce the error involved with determining absolute age from ring counts while showing accurate age class frequency distributions.

3.4.5 Regressions for estimating tree age

Table 3.7 outlines regression values for size versus age of all cored trees of the three main podocarp species. Where individual trees were not cored, their ages were determined using size versus age regression values (Table 3.7). In order to extrapolate the ages of uncored trees, a minimum regression value of R^2=0.5 was used. If the site regression for each species was below this arbitrary level, the 'all sites' value for each species was used to determine tree age i.e. regression values from Figure 3.3. No attempt was made to age stands where no cores had been collected.

Figure 3.3 shows size versus age regressions for all cored trees at all sites. Totara (R^2=0.44) and kahikatea (R^2=0.48) have higher 'all site' regression values than matai (R^2=0.28), which shows a poor correlation between size and age. The higher growth rates of totara and kahikatea contribute to the higher regression value found between size and age. Matai is more shade tolerant (Ebbett & Ogden 1998) and grows more slowly under the canopy, resulting in a lower degree of correlation between size and age.

Table 3.7 Regression values of size versus age, and values used to estimate ages for uncored trees.

A. TOTARA

Aged study sites	Regression value used	N AGED	R^2 VALUE
Mananui	Mananui	48	0.59
Payne's Ford	All sites	137	0.44
Coke Covenant 1	Coke Covenant 1	23	0.68
Coke Covenant 2	Coke Covenant 2	11	0.61
Okuti Valley	Okuti Valley	20	0.55
Okuti Valley (kanuka)	Okuti Valley both	27	0.50
Dennistoun Bush 1	All sites	11	0.44
Dennistoun Bush 2	Dennistoun Bush 2	11	0.71
ALL SITES	ALL SITES	137	0.44

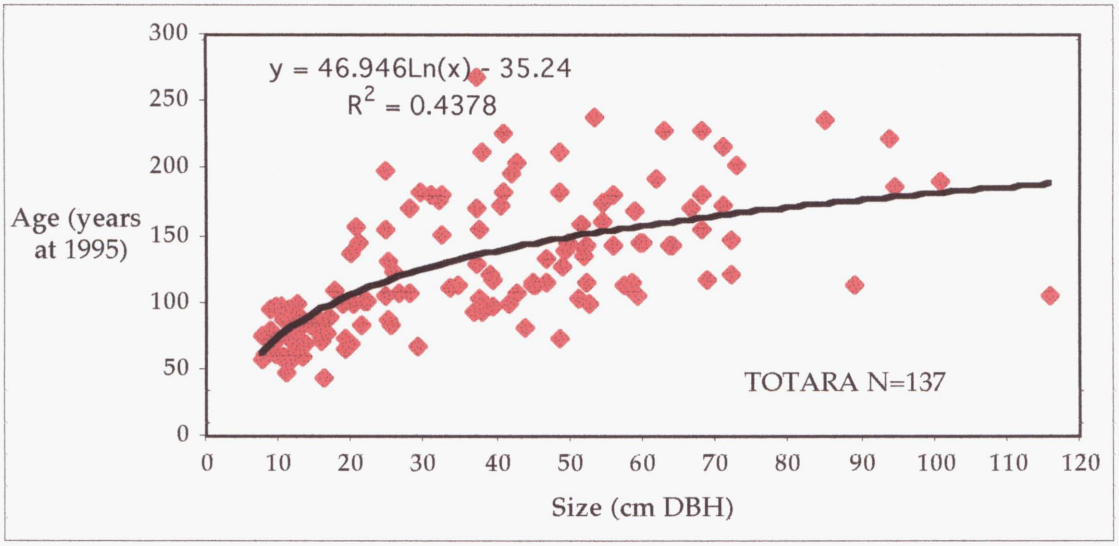
B. MATAI

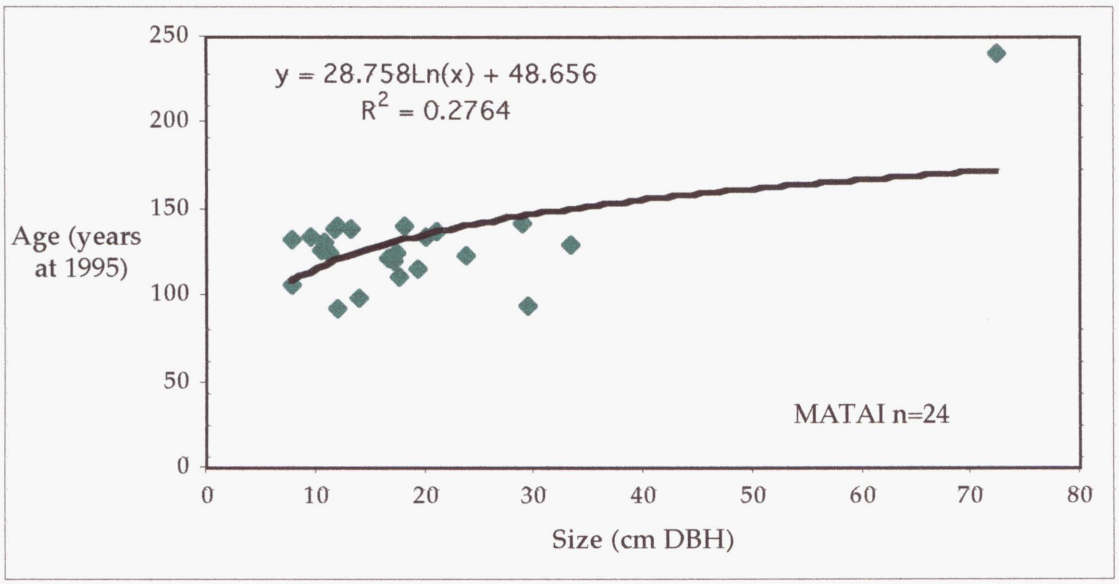
Aged study sites	Regression value used	N AGED	R^2 VALUE
Coke covenant 1	Coke Covenant both	7	0.50
Coke Covenant 2	Coke Covenant both	7	0.50
Okuti Valley	All sites	24	0.28
Okuti Valley (kanuka)	All sites	24	0.28
Dennistoun Bush 1	Dennistoun Bush both	4	0.88
Dennistoun Bush 2	Dennistoun Bush both	4	0.88
Puhi Puhi	All sites	24	0.28
ALL SITES	ALL SITES	24	0.28

C. KAHIKATEA

Aged study sites	Regression value used	N AGED	R^2 VALUE
Coke covenant 1	All sites	32	0.48
Okuti Valley (kanuka)	All sites	32	0.48
Dennistoun Bush 1	All sites	32	0.48
Dennistoun Bush 2	Dennistoun Bush 2	16	0.53
ALL SITES	ALL SITES	32	0.48

Figure 3.3 Size versus age regressions for all cored trees at all sites. Age includes adjustment value for time to reach coring height.





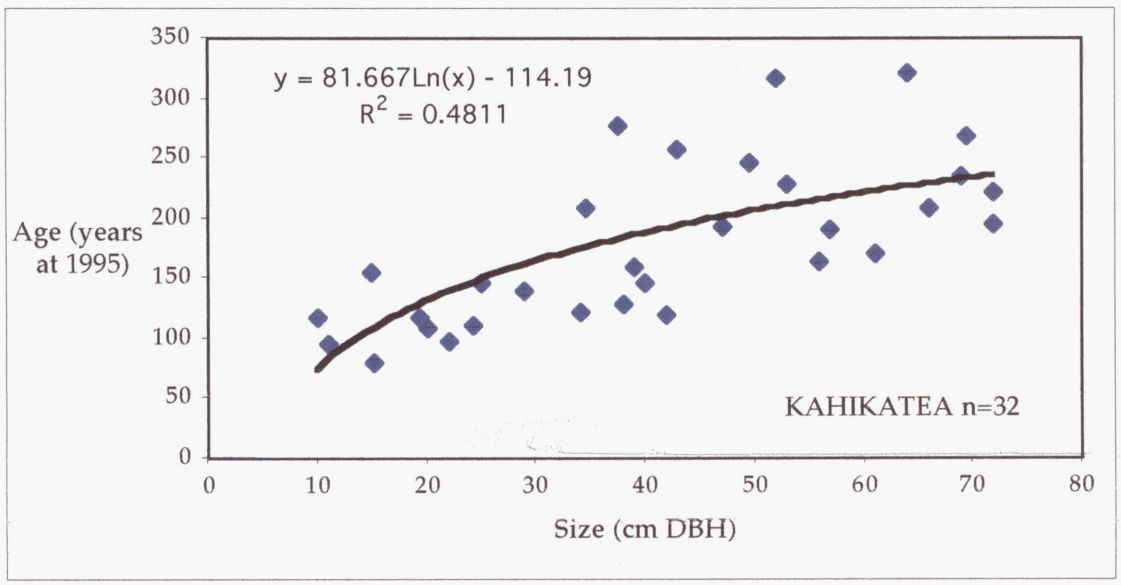


Plate 3 Field assistants (A) Dave Holliss (Mananui Bush Scenic Reserve, Hokitika) and (B) Chris Herring (Blue Duck Scenic Reserve, Kaikoura) coring totara trees.

a

b

PART TWO

THE ECOLOGY OF LOWLAND TOTARA

DISTRIBUTION & NICHE
DISTURBANCE HISTORY
STAND DESCRIPTIONS
SEEDLING ECOLOGY
SPATIAL DESCRIPTION
STAND GROWTH THROUGH TIME
OVERVIEW OF ECOLOGY

Plate 4 Almost pure matai stand on river plain, Price's Valley Covenant, Banks Peninsula.

CHAPTER FOUR
DISTRIBUTION AND NICHE

4.1 INTRODUCTION

In this chapter, the current distribution of lowland totara is investigated. Altitude, rainfall, climate, landforms, and soils are studied at a range of northern South Island sites in order to determine the niche of lowland totara. The current distribution of lowland totara throughout New Zealand is investigated via examination of the presence of lowland totara and the correlation of presence with altitude and rainfall data. The climate, landforms, and soils of the study sites are then investigated to determine the niche of lowland totara in South Island.

This chapter specifically seeks to ask the questions:
- Is lowland totara confined to a distinct niche?
- Is this niche defineable?

4.2 CURRENT DISTRIBUTION

4.2.1 Introduction and objectives

In this section, the current distribution of lowland totara is investigated in relation to altitude and rainfall. The objectives of this section are:
- To determine the distribution of lowland totara in terms of altitude,
- To determine if any correlation exists between the distribution of lowland totara and annual rainfall.

4.2.2 Methods

Distribution maps of lowland totara and *P.totara* var. *waihoensis* are presented (Fig. 4.1) using a modified system based on Franklin's (1968) *Dacrydium cupressinum* distribution maps. New Zealand is divided into 100km grids based on NZMS 260 sheetlines. Each 100km is further divided into 5km units and the presence of the

species within each 5 x 5km square noted with a symbol. Lowland New Zealand (land under 500m above sea level from topographical maps) is shown in Figure 4.2.

Distribution data were gathered from descriptive papers, Protected Natural Area Survey Reports, Department of Lands & Survey "Biological Survey of Reserves Series", National Parks Scientific Series, and herbarium specimens - Auckland Museum (AK), Auckland University (AKU), Canterbury University (CANU), Landcare Research Lincoln (CHR). The distribution maps therefore only represent documented locations of the species and so may not be comprehensive.

4.2.3 Results

Lowland totara occurs throughout all of lowland New Zealand (Fig. 4.2) except Stewart Island, being especially prevalent on Banks Peninsula, in the north-west Nelson area, and in the Manawatu. Lowland totara is noticeably absent from the Waikato and inland Southland regions, due to either extensive deforestation or climatological reasons such as low temperature. Many of the stands containing mature lowland totara are under some form of protection, although many areas are relatively small (circa 5 hectares e.g. Park & Walls 1978, Wilson 1992).

Figure 4.3 shows the average annual rainfall (mm) of New Zealand. In South Island, totara occurs mainly within the 800 - 1600mm rainfall isohyets, except for Northwest Nelson where rainfall is higher. In North Island, totara occurs within the 800 - 1600mm rainfall isohyets in the Wellington and Auckland regions. Elsewhere in North Island totara mostly occurs in the 1600 - 3200mm rainfall band.

Lowland totara is replaced by Westland totara (*P.totara* var. *waihoensis*) on the west coast of South Island. Westland totara occurs throughout Westland with an annual rainfall of 1600 - 6400mm. Trees do not reach the height of true lowland totara, possibly due to elevated nutrient leaching in the high rainfall regime.

Hall's totara is more ubiquitous in distribution than lowland totara, occurring from sea level to the montane region (Ebbett & Norton in prep.). The remaining *Podocarpus* species have more restricted distributions; *P.acutifolius* is restricted to the north-west Nelson and West Coast areas (regions of high endemism) and *P.nivalis* is restricted to the montane and alpine regions (Ebbett & Norton in prep.).

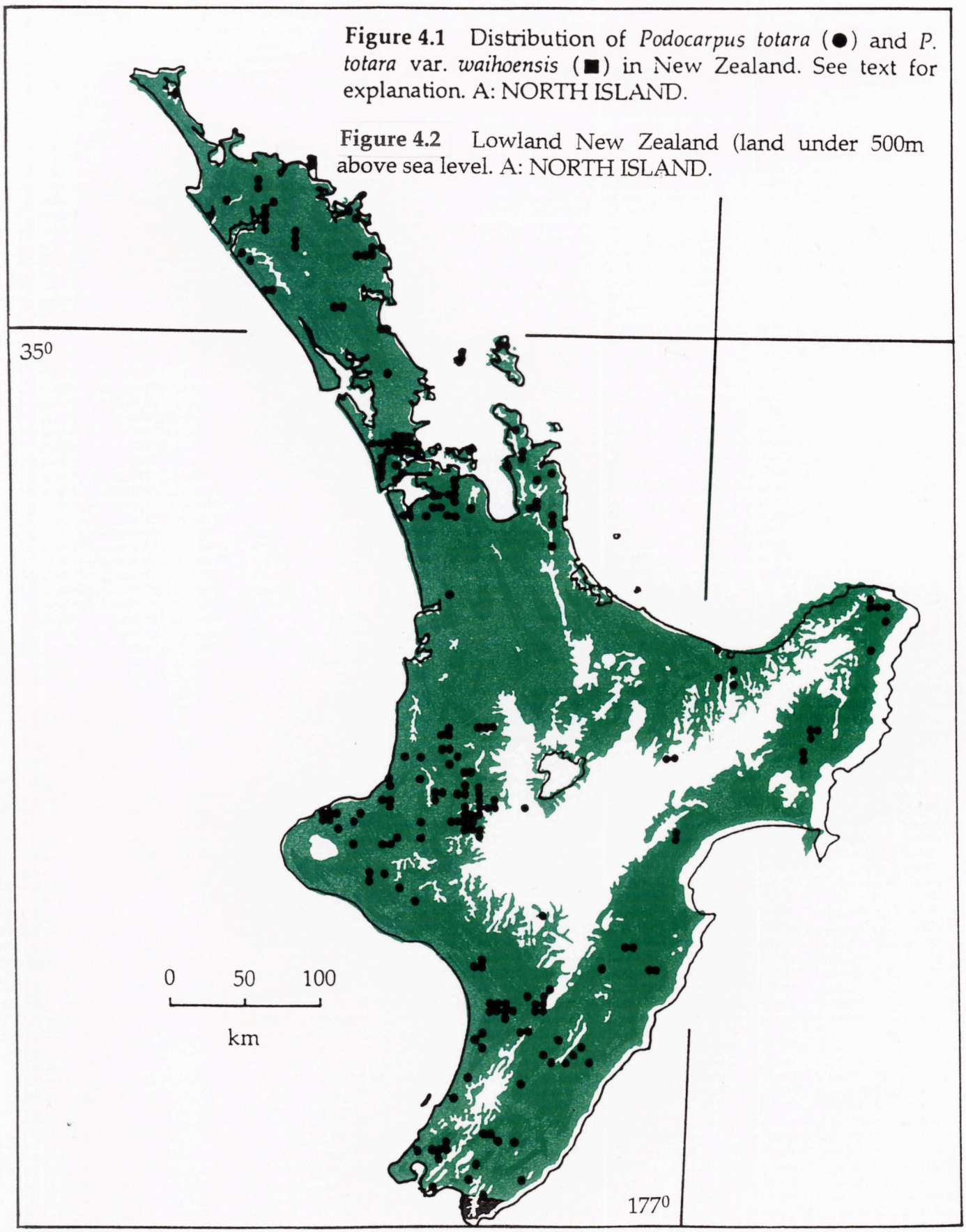


Figure 4.1 Distribution of *Podocarpus totara* (●) and *P. totara* var. *waihoensis* (■) in New Zealand. See text for explanation. A: NORTH ISLAND.

Figure 4.2 Lowland New Zealand (land under 500m above sea level. A: NORTH ISLAND.

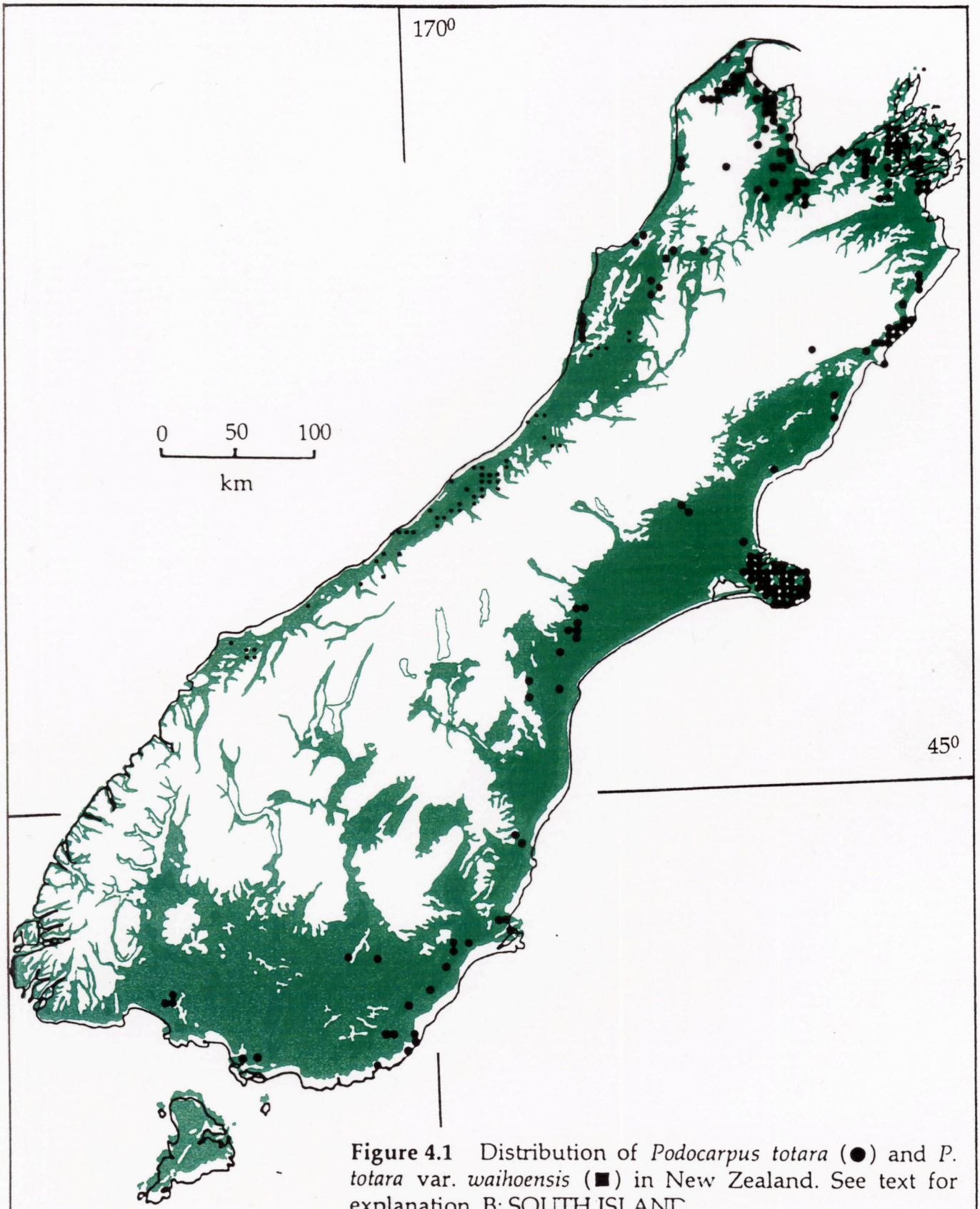
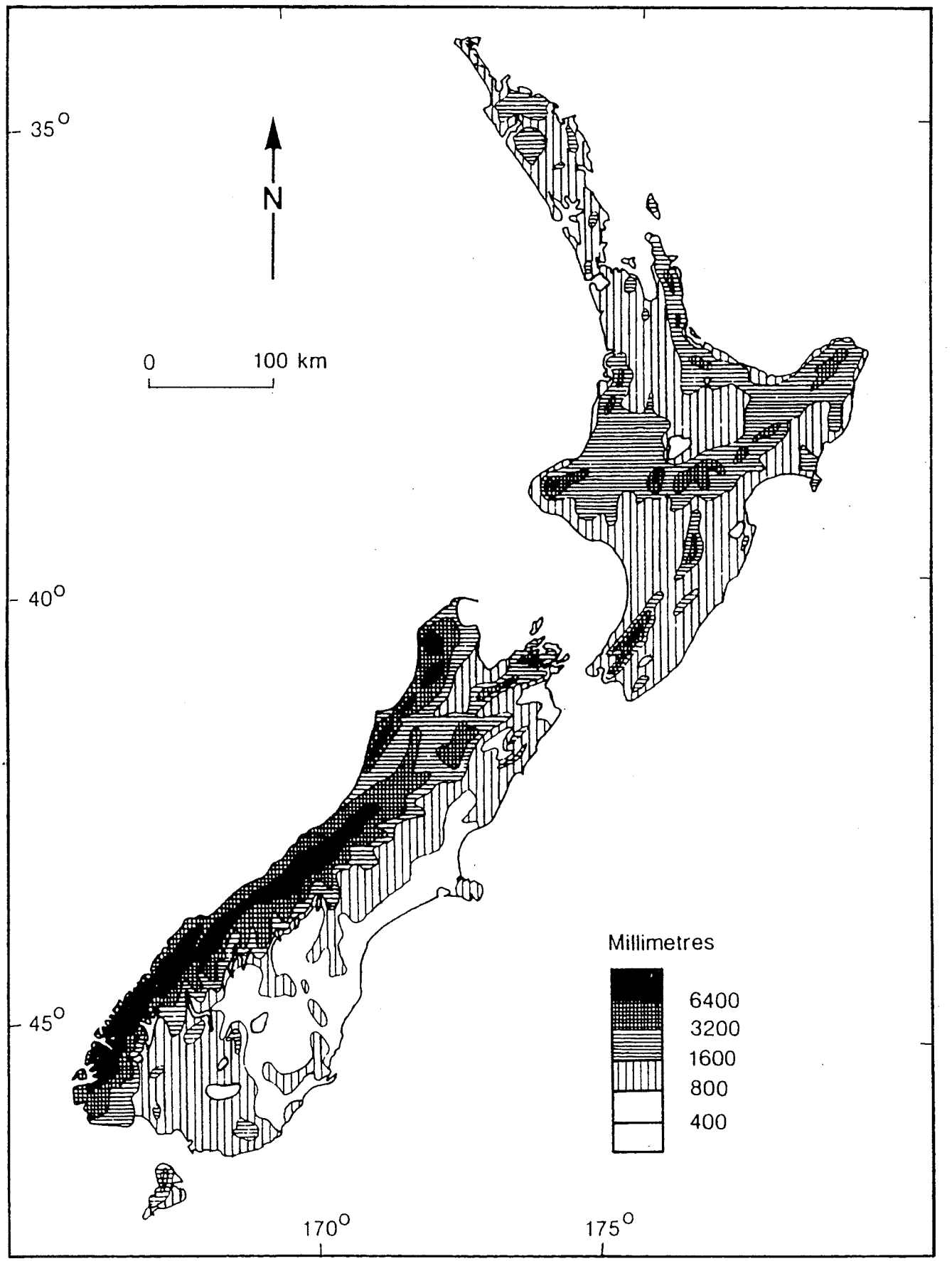


Figure 4.1 Distribution of *Podocarpus totara* (●) and *P. totara* var. *waihoensis* (■) in New Zealand. See text for explanation. B: SOUTH ISLAND.

Figure 4.2 Lowland New Zealand (land under 500m above sea level. B: SOUTH ISLAND.

Figure 4.3 New Zealand's average annual rainfall (from McGlone 1988).



4.3 STUDY SITE CLIMATE AND LANDFORMS

4.3.1 Introduction and objectives

In this section, study site climate and landforms are investigated. The objectives of this section are;

- To determine the climate in which lowland totara occurs in northern South Island,
- To determine if lowland totara is confined to distinct landforms in northern South Island.

4.3.2 Study site climate

Table 4.1 outlines fragment size and climatological data for the ten study sites. Fragment size ranges from 2-85 hectares, rainfall from 800-2700mm per annum, altitude from 0-450m (lowland to lower montane), and mean annual temperature from 10.1 - 13.2^{0}C.

Table 4.1 Fragment size and climatological data for the ten study sites. Total area data from Protected Natural Area surveys and/or DOSLI topographical maps, rainfall and temperature data from NZ Meteorological Service, altitude data from DOSLI topographical maps.

STUDY SITE (conservation status and location)	TOTAL AREA (ha)	Rainfall (mm p.a.)	Altitude (m.a.s.l.)	Mean annual ^{0}C
Nikau Scenic Reserve Punakaiki, WESTLAND	20	2400	5	12.3
Mananui Scenic Reserve Hokitika, WESTLAND	10	2700	0	11.6
Puhi Puhi Scenic Reserve Kaikoura, MARLBOROUGH	15	1400	180	12.1
Okuti Valley Scenic Reserve Banks Pen., CANTERBURY	5	1000	120	12.4
Prices Valley QEII Covenant Banks Pen., CANTERBURY	15	800	60	11.4
Coke QEII Covenant Collingwood, NELSON	2	2200	0	13.2
Payne's Ford Scenic Reserve Takaka, NELSON	50	2200	40	13.2
Denn. Bush Scenic Reserve Peel Forest Park, CANT.	41	1000	330	10.1
Blue Duck Scenic Reserve Kaikoura, MARLBOROUGH	85	1400	340	12.1
Peraki Saddle Scenic Reserve Banks Pen., CANTERBURY	75	1200	450	12.4

4.3.3 Study site landforms

Table 4.2 outlines geological information for the ten study sites. Landforms range from coastal dunes, alluvial terraces and flats, to colluvial slopes. Rock types range from marine sands and gravels, alluvium, limestone, sandstone, greywacke, loess, and basalt.

Land Use Capability classification (Van Berkel 1984) puts all sites into the lowland to lower montane altitude region and defines the sites as being of low crop suitability but high pastoral farming and/or forestry suitability. The sites with

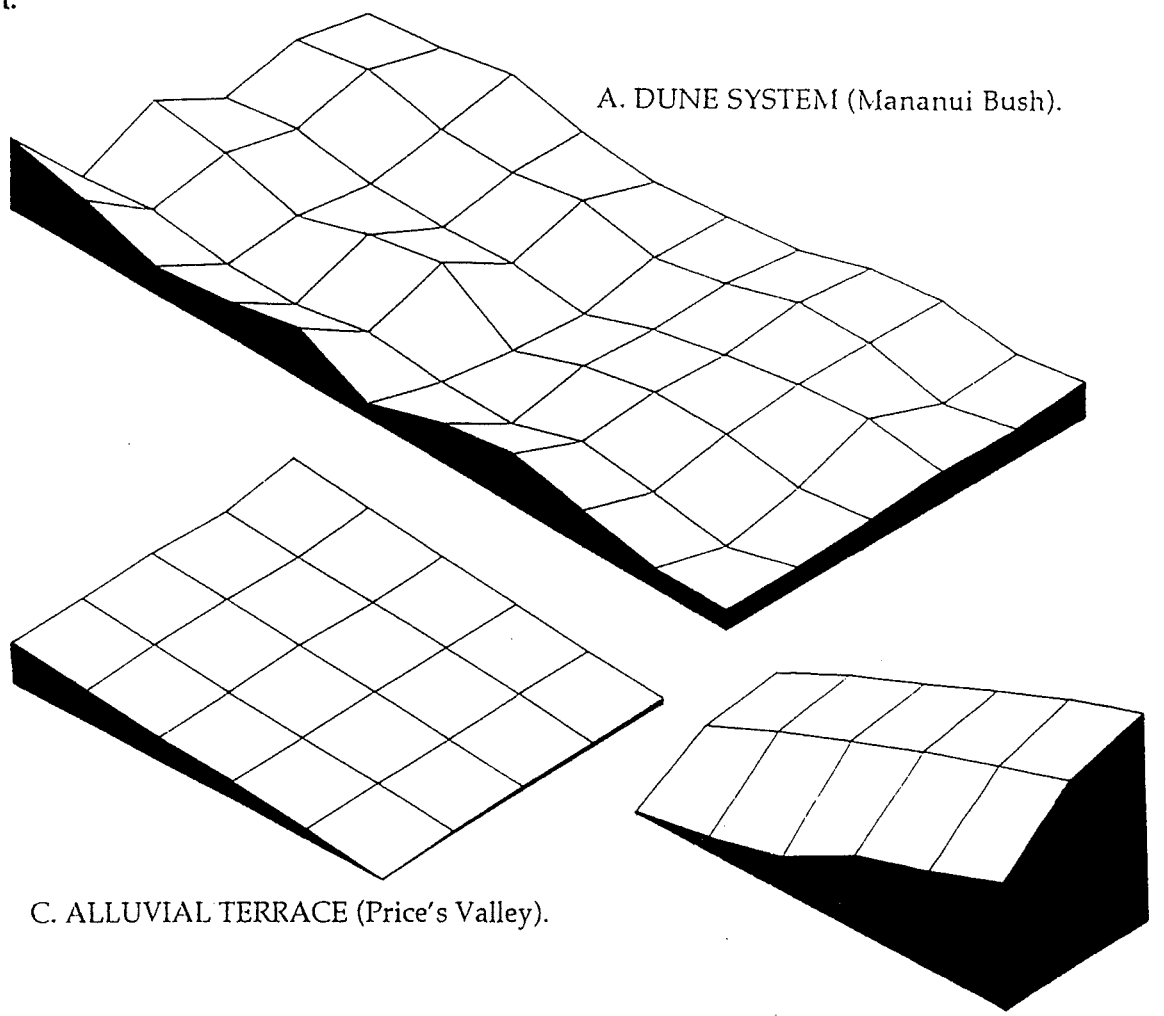
steeper slopes are classified as being suitable for pastoral or forestry land whereas less steep slopes are suitable for multiple land use.

Table 4.2 Geological information for the ten study sites. Landform data from DSIR topographical maps and/or pers.obs., rock type data from NZ Geological Survey maps, slope measured in the field (see text for explanation).

STUDY SITE (conservation status and location)	LANDFORM	ROCK TYPE	SLOPE ^{0}
Nikau Scenic Reserve Punakaiki, WESTLAND	gravel dune	post-glacial marine sand	0 - 5
Mananui Scenic Reserve Hokitika, WESTLAND	sand dune	dune sand	0 - 5
Puhi Puhi Scenic Reserve Kaikoura, MARLBOROUGH	fluvial deposit (terrace)	sandstone/ limestone	0
Okuti Valley Scenic Reserve Banks Pen., CANTERBURY	fluvial deposit (terrace)	extensive thick loess	0 - 5
Prices Valley QEII Covenant Banks Pen., CANTERBURY	fluvial deposit (river plain)	extensive thick loess	0
Coke QEII Covenant Collingwood, NELSON	alluvial fan (river delta)	river alluvium	0
Payne's Ford Scenic Reserve Takaka, NELSON	limestone bluff	Takaka limestone	0 - 20
Denn. Bush Scenic Reserve Peel Forest Park, CANT.	alluvial fan (landslip)	aggraded gravel, greywacke,	0
Blue Duck Scenic Reserve Kaikoura, MARLBOROUGH	colluvial slope	sandstone, siltstone, clay	5 - 15
Peraki Saddle Scenic Reserve Banks Pen., CANTERBURY	colluvial slope	basalt, tuff	20 - 35

Plot contour for each study site was measured during plot layout described in section 3.3.2. Slope was measured at 10m distances along each transect tape to produce a plot contour map. Slopes range from 0^0 on alluvial terraces, 5^0 on dune systems, to 35^0 on colluvial hill slopes (examples of each appear in Fig.4.4). Young/colonising stands occur on either flat or dune positions, developing, mature, and senescent occur on either flat or slope positions.

Figure 4.4 Examples of plot contour maps. A. Dune system (Mananui Bush). B. Colluvial slope (Blue Duck). C. Alluvial terrace (Price's Valley). Grids are 10m x 10m.



4.4 STUDY SITE SOILS

4.4.1 Introduction and objectives

Detailed soil analysis was conducted at each of the ten main study sites. The objectives of this section are:

- To determine the range of soils lowland totara occurs on,
- To investigate the relationships between soil type, landform, and disturbance regime.

Table 4.3 outlines likely past disturbance, soil type, and fertility level of the ten main study sites. Geological map references appear in Appendix Two.

Table 4.3 Likely past disturbance, soil type, and fertility level of the ten main study sites. Soil data from DSIR (1965), fertility level from Gibbs (1980b).

STUDY SITE (conservation status and location)	Likely past disturbance	SOIL TYPE	FERTILITY
Nikau Scenic Reserve Punakaiki, WESTLAND	dune formation	lowland yellow-brown earths	moderate to high fertility
Mananui Scenic Reserve Hokitika, WESTLAND	dune formation	yellow-brown sands	leached, low fertiltiy
Puhi Puhi Scenic Reserve Kaikoura, MARLBOROUGH	flood	lowland yellow-brown earth	moderate to high fertility
Okuti Valley Scenic Reserve Banks Pen., CANTERBURY	fire landslip	yellow-grey to y-brown earths	moderate fertility
Prices Valley QEII Covenant Banks Pen., CANTERBURY	flood	recent	moderate to high fertility
Coke QEII Covenant Collingwood, NELSON	flood	recent	moderate to high fertility
Payne's Ford Scenic Reserve Takaka, NELSON	earthquake fire	rendzina/recent on floodplain	low to moderate fertility
Denn. Bush Scenic Reserve Peel Forest Park, CANT.	flood	lowland yellow-brown earth	moderate to high fertility
Blue Duck Scenic Reserve Kaikoura, MARLBOROUGH	fire landslip	lowland yellow-brown earth	moderate to high fertility
Peraki Saddle Scenic Reserve Banks Pen., CANTERBURY	fire landslip	brown granular loam/clay	droughty, low fertility, leached

Soil type is a function of parent material and erosion processes. The type of soil present at a site is related to the landform and hence the likely disturbance regime, i.e. recent soils on alluvial terraces can occur as the result of flooding. Lowland totara occurs on soils ranging from free-draining recent pumice (central North Island) and coastal sands (Westland) to more fertile alluvial terraces, often with underlying gravel, and colluvial slopes with yellow-brown earths, yellow-grey earths, and brown granular loams (pers. obs.).

4.4.2 Soil analysis methods

One site for soil sample collection was randomly located within each study plot. Holes were dug to a depth of 75cm to investigate the soil profile. Depth of organic

layer was recorded, the presence of gravel, mottles, structure, and colour also noted.

Soil samples for analysis were collected from all sites at 5-10cm depth (in A horizon and below organic matter layer). Dennistoun Bush silt was collected from a flood event in 1994 which deposited silt 50 metres into Dennistoun Bush. All soil samples were air-dried for two weeks at approximately 20^{0}C and then passed through a 2mm sieve and stored until analysis.

Macronutrients, pH, and total percent nitrogen was analysed by the Soil Fertility Service, New Zealand Pastoral Agricultural Research Institute Limited. Macronutrient content is given in $\mu g/g$ in soil where conversion to this measure is possible, reporting units are given otherwise.

Moisture factor, percent organic matter, and percent carbon were analysed in the laboratory using the methods described by Nicholson (1984) and outlined below.

Moisture factor

A sample of air-dried soil was placed in a weighed petri dish and the weight recorded to three decimal places. The sample was then placed in an oven (100^{0}C) for 24 hours. The sample was then removed from the oven, placed in a dessicator, and reweighed when cool. Moisture factor was then calculated with the following equation;

$$\text{Moisture factor} = \frac{\text{weight air-dry soil (g)}}{\text{weight oven-dry soil (g)}}$$

Percent organic matter

The loss in weight when a soil is ignited in a furnace is an estimate of the organic matter in soil. Some inorganic constituents are also decomposed by heat but this is usually considered to be negligible (Nicholson 1984). A sample of oven-dried soil was placed in a weighed silica crucible and the weight recorded to three decimal places. The crucible was then placed in a muffle furnace at 500^{0}C for 1 hour. The sample was then removed from the furnace, placed in a desiccator, and reweighed when cool. Organic matter (% oven-dry weight) was then calculated with the following equation;

$$\text{Organic matter (\% oven-dry weight)} = \frac{\text{O.D. weight (g) - ash weight (g)}}{\text{O.D. weight (g)}} \times \frac{100}{1}$$

Percent carbon

Percent carbon is calculated from the percent organic matter content using the following equation;

Carbon (% oven-dry weight) = 0.58 x % organic matter

4.4.3 Soil analysis results

Figure 4.5 outlines the soil analysis results. All results presented are for A horizon samples. In general, the level of fertility ranges from lowland yellow brown earths (highest) to yellow brown sands (lowest). Nutrient content and its effect on vegetation composition is discussed by Gibbs (1980a). Podocarps are seen to occur on the most fertile soil types which are also the youngest. Organic matter, pH, total nitrogen, and carbon levels follow a similar trend for all sites. With the exception of Nikau, Mananui, and Dennistoun Bush silt (discussed below), all nitrogen values fall into the medium or high categories described by Gibbs (1980b). Carbon to nitrogen ratios are consistently high, indicating the moderate to high fertility status of these soils.

Three outlying sites are present, one with consistently high nutrient levels (Nikau Reserve) and two with consistently low nutrient levels (Dennistoun Bush silt and Mananui Bush). Nikau Reserve is a series of gravel dunes where soil formation is in its early stages (Plate 5). Soil analysis was conducted on particles collected from around the gravel and mainly consists of organic matter, hence the elevated nutrient levels. Overall, the soil would be considered to be of low fertility but with excessive drainage. Plate 6 shows the prograding gravel dune position of the site.

Figure 4.5 Nutrient analysis for the main study sites. A. Percent total nitrogen, moisture factor, pH.

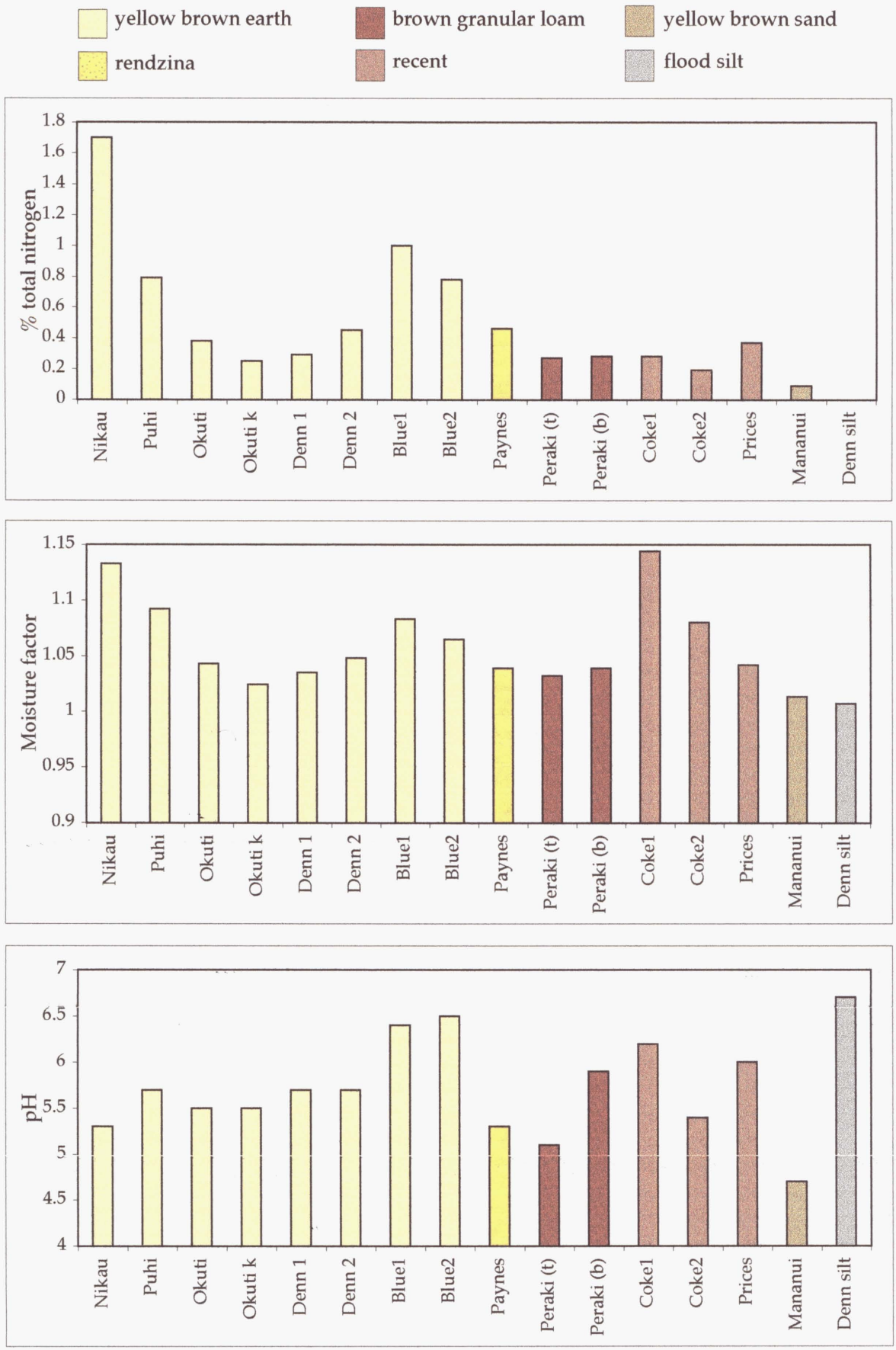
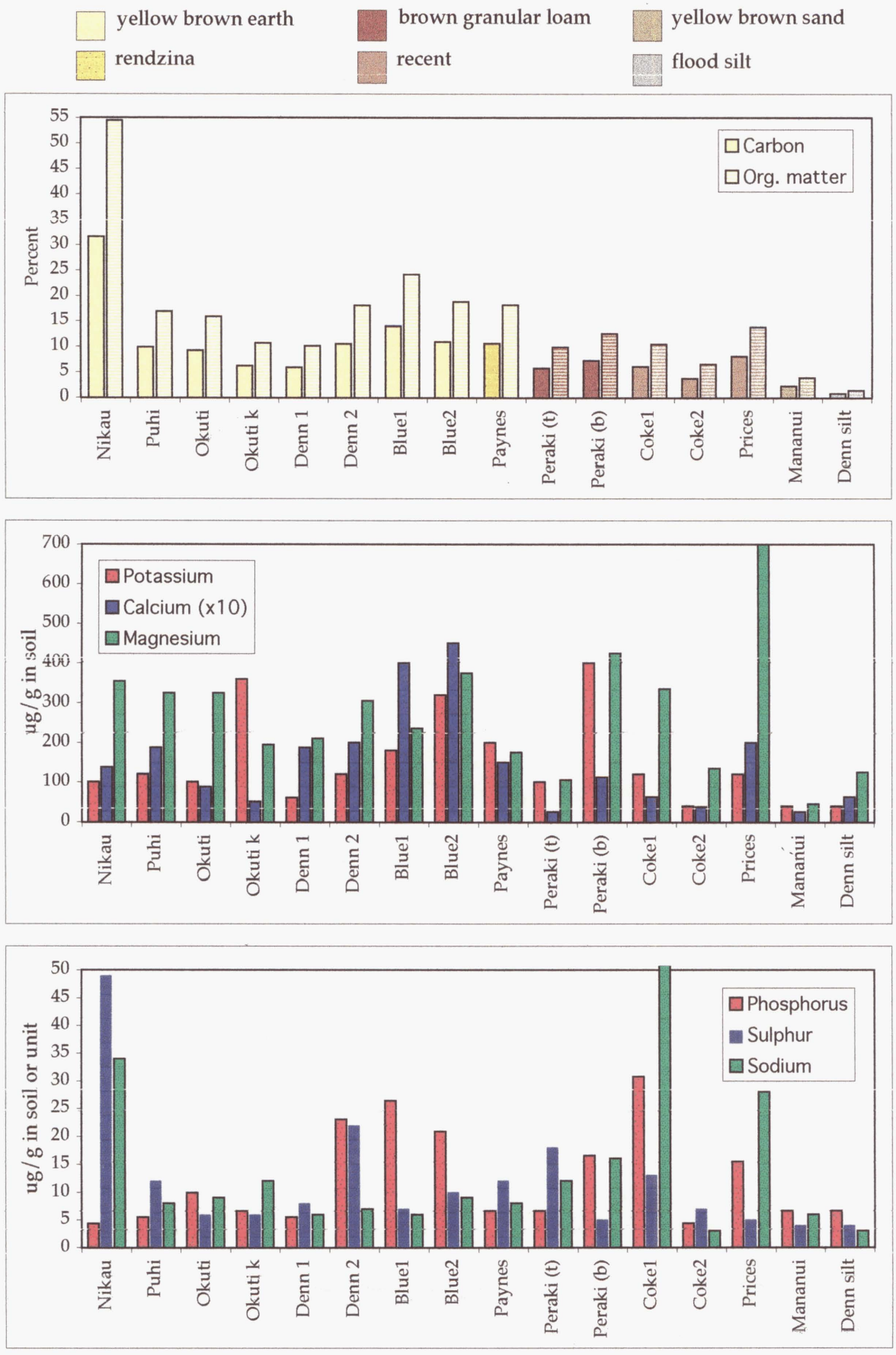


Figure 4.5 Nutrient analysis for the main study sites. B. Carbon/organic matter, potassium, calcium, magnesium, phosphorus, sulphur, sodium.



In the two study sites in Westland (Nikau Reserve and Mananui Bush), totara is acting as a primary coloniser on prograding dunes with low fertility but high drainage due to the presence of gravel or sand. The low fertility status accounts for the presence of rimu in these stands. In wet districts rapid leaching of soils largely confines lowland totara to recent alluvium and tephra deposits, being replaced by Hall's totara on less fertile soils and at higher altitudes (Wardle et al 1983).

Nutrient analysis shows that the silt deposited in Dennistoun Bush has no significant nutrient input to the soils present. The effect of the silt is physical in nature i.e. decreases drainage due to fine particles. The effect of this flooding regime is discussed further in section 5.3.4.

Gravel ranging from 1 - 10cm diameter was noted to occur in the free-draining soil profiles at Puhi Puhi Reserve, Nikau Reserve, Price's Valley, and Dennistoun Bush. This represents the presence of gravel at four out of ten sites.

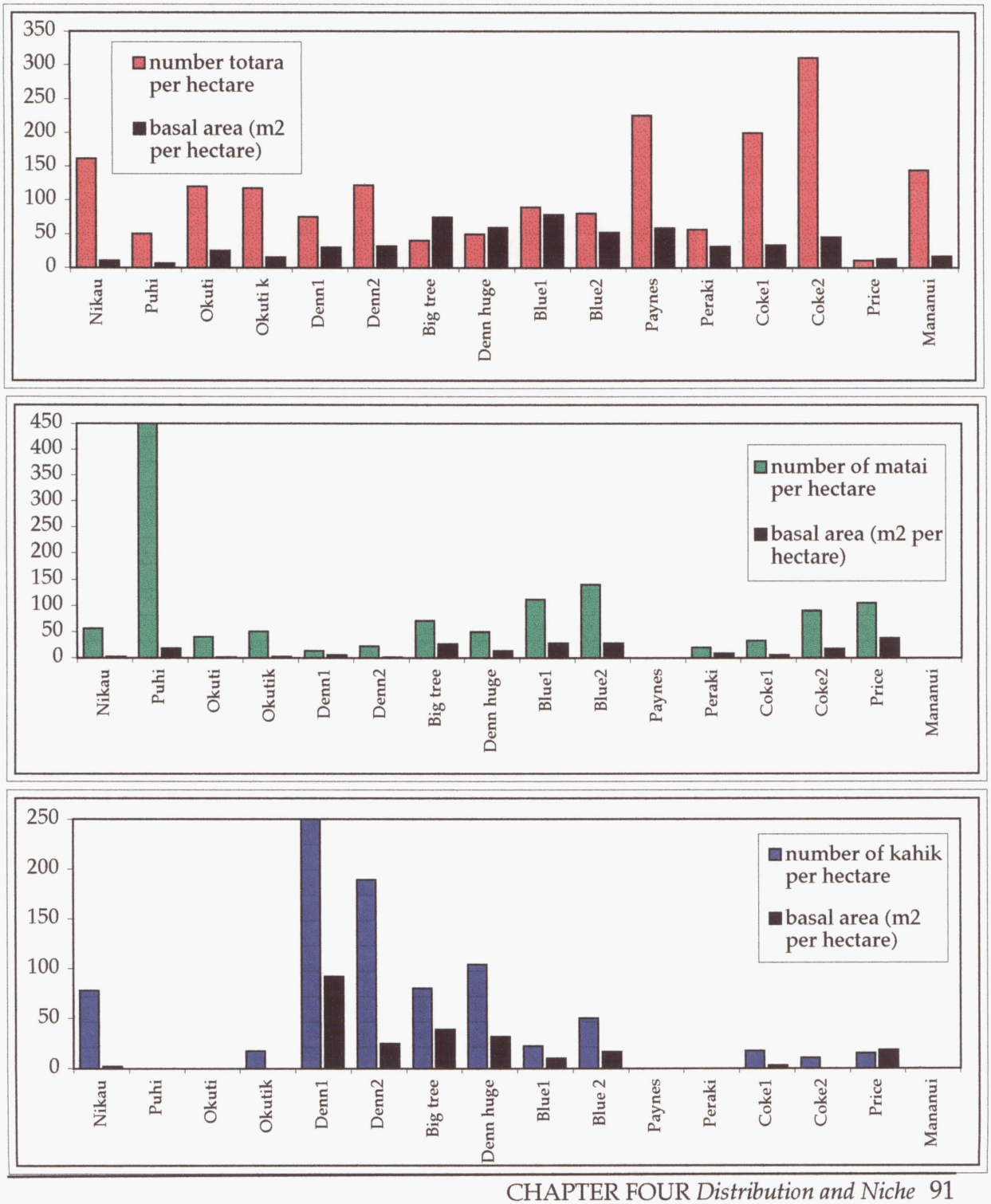
Calcium and sodium are interlinked nutrients, sodium displaces calcium and sites with high levels of one are usually low in the other (Mollison 1992). The high sodium levels of Price's valley and Coke 1 may be due to salt water flooding. Elevated calcium levels of Blue Duck 1 and 2 may be due to the older surface age or the vicinity of limestone parent rock. The low magnesium levels of Coke 2 and Peraki top are due to low pH (Tisdale et al 1985). The elevated magnesium level of Price's Valley could be due to groundwater being high in magnesium (Tisdale et al 1985).

Potassium is deficient in free-draining sandy coastal soils such as Mananui but is not leached from other soil types (Mollison 1992, Tisdale et al 1985). High levels of potassium can be a function of acid soils (Tisdale et al 1985). Phosphorous is not lost by leaching as in sandy soils and elevated levels are due to either naturally high levels in subsoil, high pH, high calcium, or proximity to top dressing (Tisdale et al 1985).

Figure 4.6 shows number of adult stems per hectare and basal area values for all sites, arranged in the same order as Figure 4.5. i.e. from yellow-brown earths through to yellow-brown sands. It is interesting to note that matai and kahikatea are absent from stands with rendzina (Paynes Ford) or yellow-brown sand (Mananui) soils. Kahikatea is also absent from stands containing brown granular loams (Peraki). Of the eleven stands where kahikatea occurs, all are recent or yellow-brown earth soils. Number of adults and basal area per hectare are greatest

on the yellow-brown earth soils. In total, kahikatea occurs in 85% of stands containing these soils. Yellow-brown earths and recent soils show moderate to high fertility, the highest pH, and the highest moisture factor of the study site soils sampled (see Fig. 4.5.). Totara occurs on all soil types, the most dense stands being on recent and rendzina soils (Fig.4.6.).

Figure 4.6 Number of adult stems (≥10cm DBH) per hectare and basal area values (m^2 per hectare, saplings and adults) for all study plots.



4.5 DISCUSSION

Totara appears to be confined to areas with rainfall >800mm per annum. Totara dominated stands mostly occur at below 500m above sea level, although in Southland this level drops to approximately 300m due to the lower temperatures of the region (Figure 4.2). On Banks Peninsula, Hall's totara replaces lowland totara at around 400 to 450m and in this altitude band a hybrid swarm occurs (section 3.2.3).

Of the study sites, rainfall ranges from 800mm per annum on Banks Peninsula to 2700mm in Westland. In Westland, totara dominated forest occurs only on free-draining soils such as gravels and sands (McSweeney 1983). The occurrence of totara in low rainfall areas such as inland Canterbury indicates its drought tolerance ability (section 1.3.2).

Climate has several components which influence the development of soils. The weathering of parent materials increases with temperature. Rainfall causes both erosion and leaching of nutrients, which is in turn affected by the soil's drainage properties (Metson 1974). Vegetational composition has been shown to be a function of degree of weathering and intensity of leaching (Gibbs 1980a).

Mananui Bush has a high rainfall (circa 2800mm per annum) and so the well drained lowland yellow-brown sandy soil is extremely leached. Mananui Bush has a sequence of vegetation which ranges from flax and gorse on the foredunes to tall totara dominated forest on the reardunes (see Plate 6). This indicates progressive dune age and that the system is prograding. One study on dune/vegetation relationships showed that with increasing surface age, pH declines and organic matter increases, allowing broadleaves and eventually podocarps to colonise on 1,000 year old dunes (Smith et al 1985).

Landform and topography are major determinants of soil type, drainage properties, and hence vegetation type. Several studies indicate that disturbances such as landslides and windthrow rejuvenate soils whereas stability leads to old, infertile, and often poorly-drained soils (Stewart et al 1993, Rogers 1995). Vegetational composition has been shown to be a function of the magnitude and frequency of disturbances (Stewart et al 1993), increasing soil depth and reduced drainage status with surface age (Rogers 1995), and topography and its effect on drainage (Norton 1994).

Lowland totara appears to be confined to distinct landforms. The most dense stands occur on fluvial deposits which include alluvial terraces and fans (see Plate 2), river plains (see Plate 1), and coastal dunes (see Plate 6). As fluvial situations are subject to repeated flood events as well as river course changes this indicates that disturbance is a major factor in the distribution of totara dominated stands. Large scale disturbance can occur if flooding is combined with earth movement. Totara was also found on a limestone bluff in Takaka which was originally tectonically uplifted and presently subject to accelerated erosion.

Wardle (1974) discusses the establishment of kahikatea on alluvial terraces in south Westland and states that thickets of *Coprosma propinqua* and *P.totara* var. *waihoensis* provide shelter for kahikatea seedlings, with totara being more dominant on dry, stony ground. The presence of totara on shingle ground in Westland is also noted by Foweraker (1929). In the present study, gravel was found in the soil profiles of 40% of the main study sites, all of which are alluvial or coastal sites. Recent alluvial soils characterise the presence of totara/kahikatea/matai forest; on stonier and better drained soils kahikatea is equalled or exceeded in abundance by the other podocarps (Wardle 1974). As podsolization and gleying leads to decreased soil fertility, rimu gradually replaces kahikatea or, on better drained sites near the mountains, lowland totara. The present study indicates that kahikatea may increase in abundance on the more fertile yellow-brown earths and recent soils (see Fig.4.6.).

Slope and topography influence both microclimate and local variation in soil properties and moisture availability, and hence vegetation composition (Leathwick & Rogers 1996). Stable ridge soils can be expected to be less fertile than lower slope soils which are subject to periodic inputs of colluvium or alluvium (Campbell 1973, 1975, Gerard 1981), soils on mid-slopes are more variable. Steep slopes are generally more unstable and have shallow, immature soil due to the constant erosion process (Metson 1974). Soils in upper slope positions are likely to be more drought prone and this can produce marked differences in vegetation composition (McQueen 1961).

Less dense podocarp stands occur on colluvial slopes such as Blue Duck and Peraki Saddle (see Fig.4.6., Plate 7) and in these situations lowland totara becomes confined to the most fertile soils and areas which suffer large scale disturbance (pers.obs.). In Blue Duck Scenic Reserve, lowland totara appears to be more dominant on ridges and upper slopes whereas kahikatea is prevalent on lower slope and gully positions. Soil analysis results show top of the slope soil at Peraki Saddle to have lower nutrient levels and pH than those found at the bottom of the

slope. Plate 7 shows the colluvial slope situations of Blue Duck and Peraki Saddle Scenic Reserves.

In New Zealand, naturally fertile soils are of limited extent (Wardle 1991), examples being recent, fine-textured alluvial soils (such as on the river plain at Coke Covenant), and colluvial soils derived from basaltic or calcareous rocks (such as at Blue Duck Scenic Reserve). Wardle (1991) states that these fertile soils will be colonised by adventive species adapted to a vigorous regime of nutrient recycling to the exclusion of native species, whereas semi-fertile soils include younger or less leached soils and can support vegetation such as totara/matai forest.

The distribution of lowland totara dominated stands appears to be a function of several interlinked site characteristics such as climate, landform, drainage, disturbance regime, and soil type, with an altitudinal limit superimposed. Lowland totara appears to be confined to semi-fertile or fertile soils which are the result of landform and disturbance i.e. flood events on a river plain. The competitive advantage of adventive species on fertile soils may pose a problem to the future regeneration of lowland totara-dominated forest.

Lowland totara was once a common forest tree throughout lowland New Zealand. Since the arrival of humans, lowland forest has been severely reduced in extent - only circa 1% of the original lowland forest cover remains in many areas of New Zealand. The preferred position of lowland totara on fertile alluvial plains and terraces made it vulnerable to clearance as this land was considered valuable for conventional agricultural practices. Lowland totara now occurs in a highly fragmented state with many surviving stands being of limited extent.

Plate 5 Young gravel soil with colonising dense mixed podocarps at Nikau Scenic Reserve, Punakaiki.

Plate 6 Colonising stands at (A) Mananui Bush Scenic Reserve, Hokitika (sand dunes) and (B) NIkau Scenic Reserve, Punakaiki (gravel dunes).

A

B

Plate 7 Colluvial slope stands - (A) Dense mixed podocarps in Blue Duck Scenic Reserve, Kaikoura, and (B) *P.totara*/matai/*P.hallii* forest at Peraki Saddle Scenic Reserve, Banks Peninsula.

A

B

CHAPTER FIVE
DISTURBANCE HISTORY

5.1 INTRODUCTION AND OBJECTIVES

The relatively new paradigm in forest ecology of disturbance-mediated forest composition indicates that disturbance plays a major factor in the regeneration of many species (Pickett & White 1985). Lowland totara is considered to be a colonising species in response to disturbance (e.g. Greenwood 1949, Beveridge 1983). Seedlings respond well to increased light levels, such as those found after canopy disturbance (Ebbett & Ogden 1998). The highly disturbed landform positions of totara such as alluvial river plains also indicate the importance of disturbance in the regeneration of this species.

In the present study, an effort was made to identify the likely past disturbance events at each site in order to determine causal stand mechanisms and the role of disturbance in the regeneration of this forest type. The objectives of this chapter are:

- To determine whether disturbance is a significant factor in the regeneration of lowland totara forest,
- If so, what are the disturbance types and scale.

5.2 METHODS

All evidence of past disturbance encountered while surveying the sixteen plots at the ten study sites is presented below. The active alluvial fan (a landform commonly associated with lowland totara forest) at Dennistoun Bush has a well documented disturbance regime and so is discussed in detail. Landform and soil type were the primary identifiers of the disturbance regime (i.e. river plains with recent soils are obviously experiencing periodic flood events, prograding dune systems with gorse indicate primary colonisation etc). Literature review has also provided information on dates of forest fires or clearance.

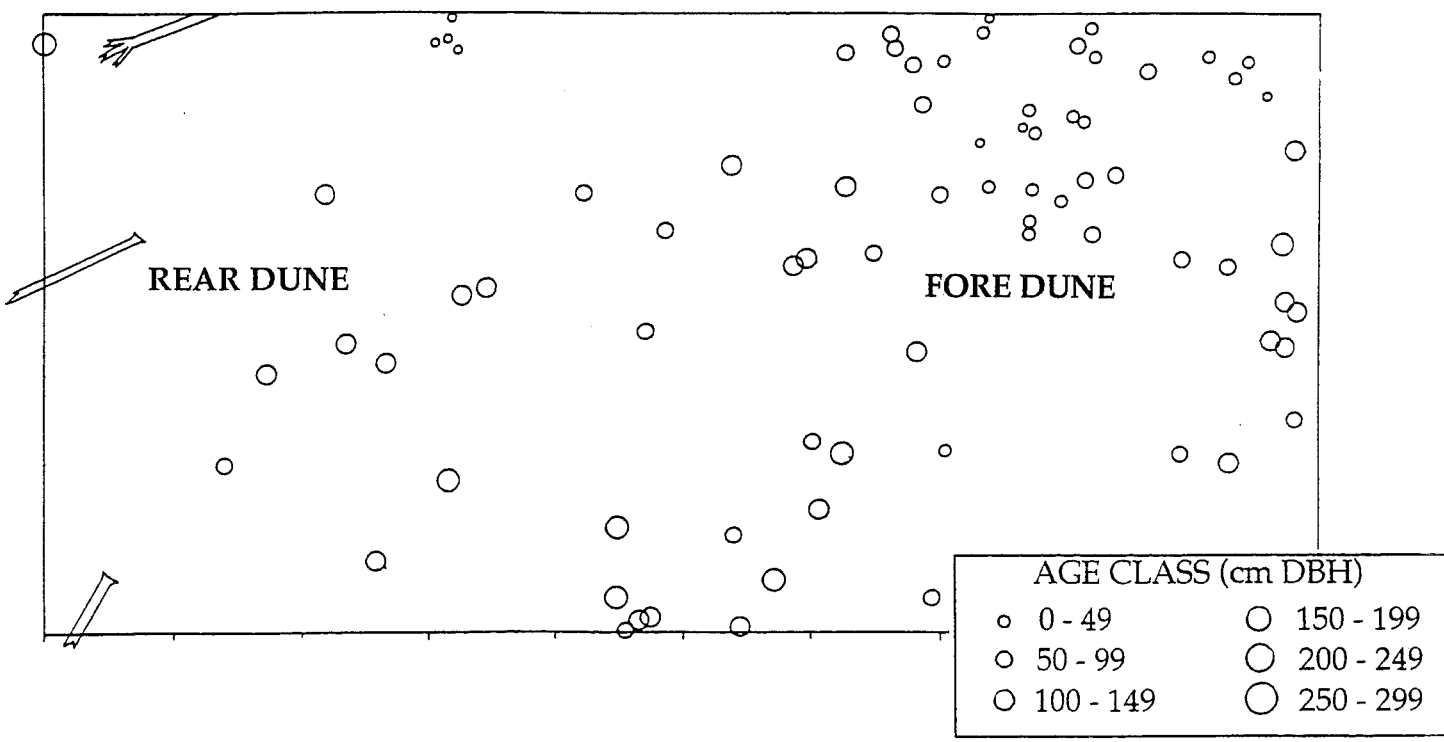
In order to determine the possible effects of different disturbance events, it was necessary to age the events themselves and the trees which may have regenerated as a result of the event. One method of ageing disturbance events is to age the trees on each disturbance-generated surface. Tree ages were determined both directly using core counts, adjusted for growth to coring height and weighted for reliability, and indirectly for uncored trees using regression equations of aged trees at each site (Fig.3.3.).

5.3 RESULTS

5.3.1 Primary colonisation

Figure 5.1 shows tree locations and ages at Mananui Bush, Westland. Lowland totara is seen to be colonising forward on this prograding dune system (see Plate 6). Gorse and flax, with totara seedlings underneath, occur on the foredunes to the seaward of the study plot. Gorse is now widespread in New Zealand and can play an important role in forest development i.e. as a nurse crop (Wilson 1994). It also acts to fix nitrogen in the soil and so may be conditioning the foredunes for invasion by secondary vegetation. Older, secondary totara forest occurs on the rear dunes which are subject to windthrow.

Figure 5.1 Tree locations and ages at Mananui Bush, Westland.



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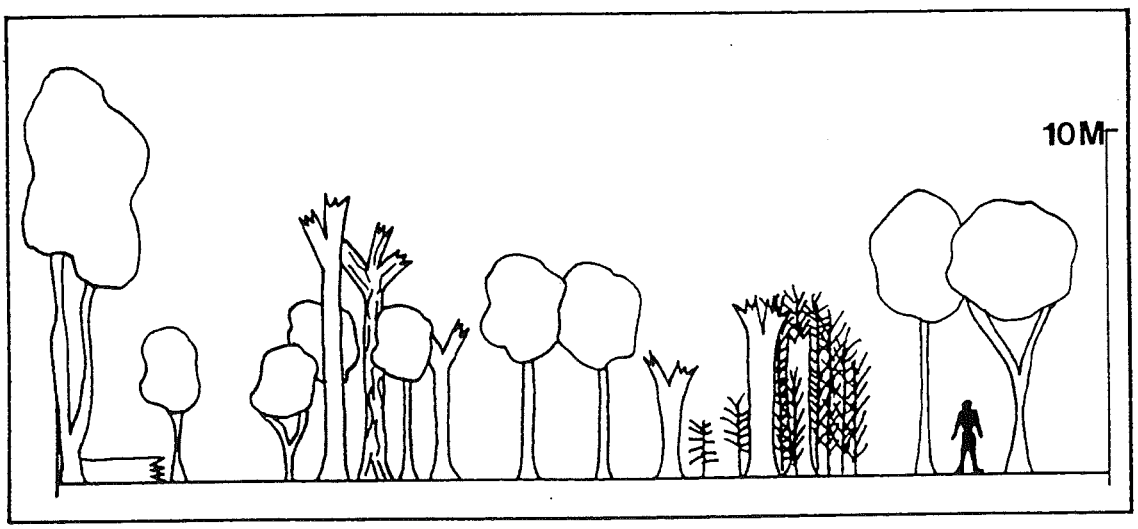
Totara at Nikau Reserve, Westland, also appears to be colonising dunes (see Plate 6), with gorse and flax on the foremost dunes and higher with more vertically structured vegetation on the inland dunes. The disturbance regime at these sites is the creation of new dune areas for colonisation. Totara is able to act as a primary coloniser, occurring with the gorse, due to its high light requirement.

5.3.2 Windthrow and gap-phase regeneration

Evidence of gap-phase regeneration was observed on the rear dunes within the study plot at Mananui Bush Scenic Reserve. This stand is buffeted by prevailing on-shore winds and the canopy is wind-swept and closed. The forest edge is very abrupt due to this wind exposure and the sealing effect of the closed canopy. This dune system has older and taller totara trees on the rear dunes which are subject to wind-throw by the prevailing winds. Figure 5.2 shows the canopy gap with totara saplings at Mananui Bush. While the main form of disturbance at totara dominated sites appears to be catastrophic, totara may be able to regenerate in large canopy gaps due to elevated light levels.

Figure 5.2 Profile diagram showing canopy gap with totara saplings at Mananui Bush Scenic Reserve, Westland.



5.3.3 Fire and landslip

At Okuti Valley, Banks Peninsula, fire is the likely stand initiator due to the presence of kanuka and dates of forest clearance (see section 7.3.1 and Fig.4.7). Forest clearance and fires would have been lit in this area around 1830 - 1870 (Ogilvie 1992). This site also appears to be on an old landslip site which may have been the original disturbance mechanism leading to lowland totara dominance.

Blue Duck Scenic Reserve also appears to be on an old landslip site (see Plate 7). Old landslips may be associated with fault movements or rockfall and are an important initiator of totara dominated stands due to the fresh soil which is deposited on the slip toe. Totara dominated stands may then remain dominant through time due to fire or other disturbance events which favour totara and its associated species.

5.3.4 Flood

The position of lowland totara dominated stands on alluvial fans and river plains exposes them to regular flood events. Both Coke Covenant stands occur within 50m of the main branch of the Aorere River (see Plate 8) and several minor channels bisect the stands. Soil is free-draining river sand and silt of recent origin which is relatively dry after one day following 125mm of rain (Mr Coke pers.comm.). Local residents recount a large flood in the area in November 1994 (Mr Coke pers.comm.). Price's Valley and Puhi Puhi are also situated within 50m of major rivers and so would be expected to experience a periodic flood regime. These sites also have recent alluvial soils. The presence of abundant titoki trees in Price's Valley is further evidence of disturbance (Hugh Wilson pers.comm.).

Peel Forest Park, inland Canterbury, provides an excellent example of a regular flood regime with resulting forest disturbance. In January 1975 a log dam in the upper catchment region broke during a high rainfall event (245mm in a 2 hour period) and a flood surge was sent down Kowhai Stream (Hall 1993). This surge broke the banks of Kowhai Stream, cascaded through Blandswood settlement, destroyed several houses, and took the lives of four children. The surge then continued into Dennistoun Bush, depositing a 1m thick layer of silt and gravel (Hall 1993). This tragedy instigated investigations into the flooding regime in the area (Massam 1986, Hall 1993).

Plate 9 shows two small deposition events, in 1986 (photo courtesy D.Buchannan) and 1993 (pers.obs.). The Department of Conservation shelter has since been removed. Note that the podocarp trees in the foreground in 1986 have since died. The swath zone created by the 1975 flood surge killed many trees due to root damage and allowed the noxious weed 'old man's beard' to enter (Massam 1986). Twenty years after this event, 'old man's beard' has penetrated at least 100m into Dennistoun Bush, retarding regeneration and destroying the canopy species due to shading and strangulation.

There is evidence (Hall 1993) that floods such as the 1975 event occur regularly in this catchment and debris can be deposited up to 400m into Dennistoun Bush, creating these 'swath zones' where tree death occurs. Hall (1993) suggests that podocarps are regenerating around the edge of the swath zones but that regeneration within them is non-existent. The occurrence of tree fushcia on the edges of Kowhai Stream is further evidence of periodic disturbance. Abundant kahikatea regeneration was seen on the edges of Kowhai Stream, possibly as a result of silt deposition during recent flood events (pers.obs.).

Hall (1993) surveyed the Kowhai Stream area and found different flood surfaces characterised by gravel and silt deposition. Other evidence, such as tree scarring and deposition smothering, indicated catastrophic flood events in the last 150 years. Hall (1993) then used podocarp tree ages to age these flood events, dated at circa 1740, and 1840A.D. Hall (1993) suggests that erosion periods, landslips, and resulting flood events in the Peel Forest catchment may be related to earth movements. Recent work by William Bull, University of Arizona, uses a lichenometric method to date Alpine Fault movements (Bull 1996). Thirty thousand lichen size measurements were used to develop a coseismic rockfall model for South Island. Calibration of lichen growth rates provided a way to date prehistoric rockfalls and landslides caused by earthquakes with 95% confidence level uncertainties of ±3 to ±13 years (Bull 1996).

Results show that four pairs of closely spaced major earthquakes have occurred with clocklike regularity every 250 years or so (1748, 1489, 1226, and 967A.D.), and that the next magnitude 8 earthquake is due soon (Bull 1996). Earthquake-caused landslides have been shown to maintain some tropical rainforests in successional stages and be an important component of the disturbance regime (Garwood et al 1979). The most recent earthquake date of 1748A.D. (Bull 1996) is remarkably similar to the estimated flood event of circa 1740A.D. (Hall 1993), suggesting that the flood event was a result of an earthquake initiated landslip blocking the catchments upper reaches and then subsequently failing to release flood waters.

Figure 5.3 shows the flood surfaces which deposited silt and gravel into Dennistoun Bush (Plate 9) and the position of the study sites. The positions of several large (circa 2-3 meter diameter) totara trees is also shown. These large totara are on the edge of the circa 1740A.D. flood surface and were possibly large enough at the time not to have been damaged by this event. Dennistoun Bush 2 occurs on the same circa 1740A.D. surface and is considered to be even-aged, providing evidence for cohort regeneration in response to this large disturbance event.

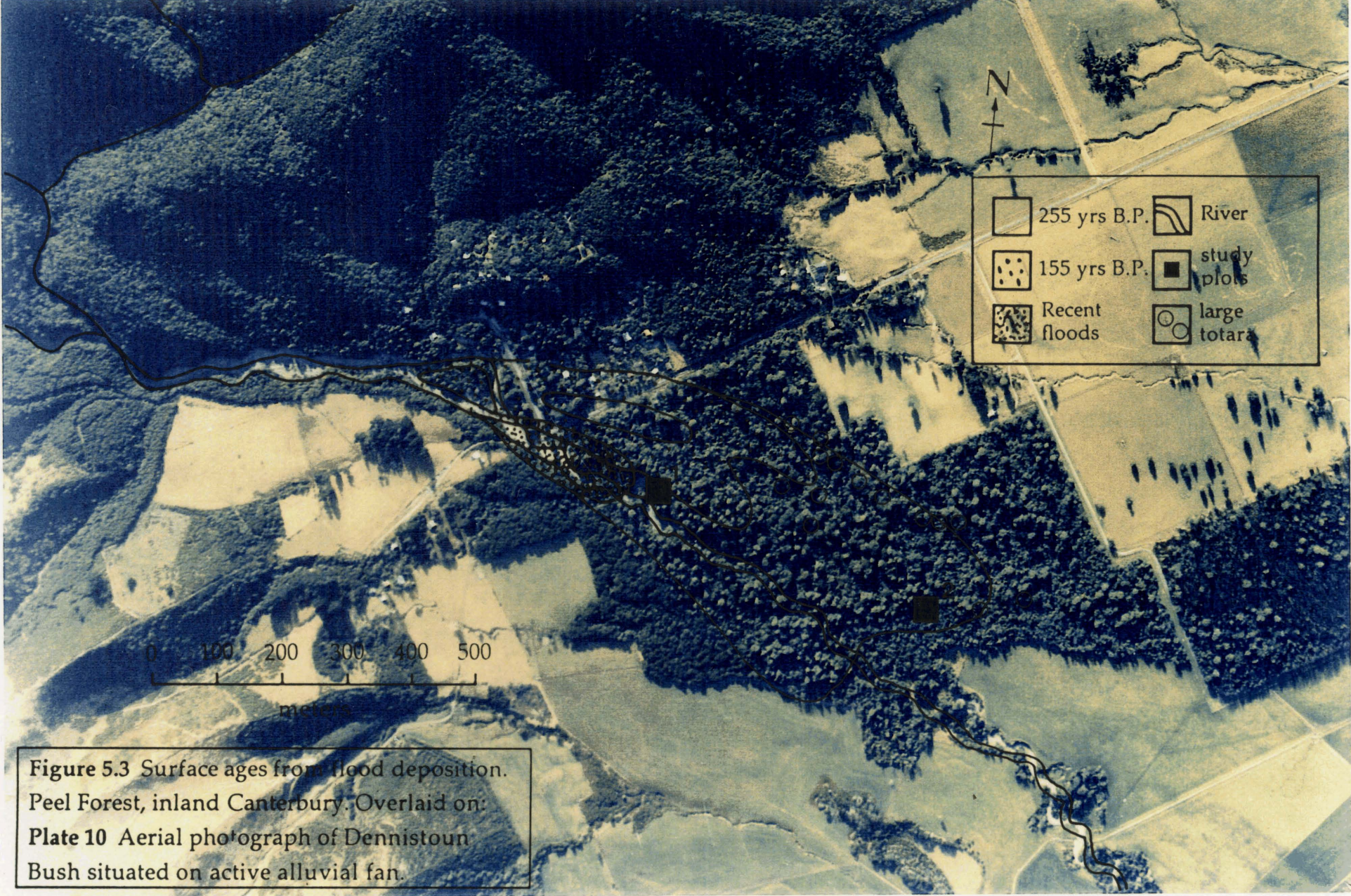


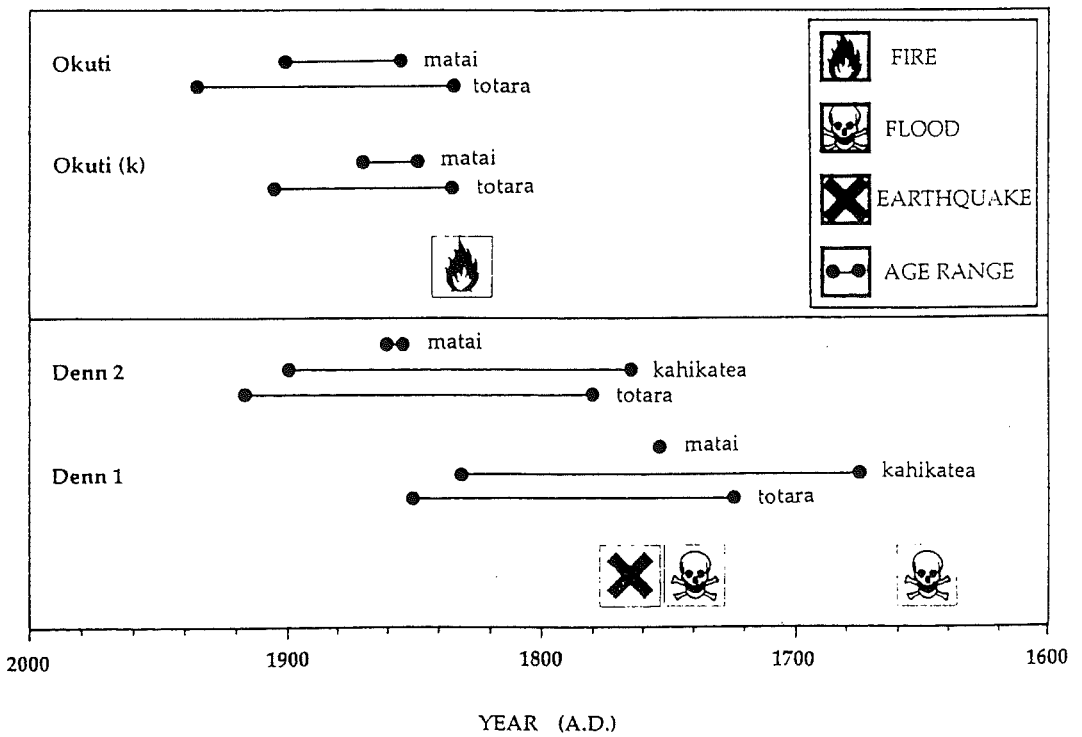
Figure 5.3 Surface ages from flood deposition. Peel Forest, inland Canterbury. Overlaid on: **Plate 10** Aerial photograph of Dennistoun Bush situated on active alluvial fan.

Dennistoun Bush 1 is approximately 100 years older than Dennistoun Bush 2 and occurs on an older flood surface (Fig.5.4). It is also considered to be even-aged and may have been mature enough to survive the subsequent flood in circa 1740A.D. A layer of gravel was encountered 50cm under Dennistoun Bush 2, providing evidence of a flood surface.

5.2.5 Disturbance chronology

Absolute ages and disturbance chronologies for Okuti Valley and Dennistoun Bush appear in Figure 5.4. Both plots at Okuti Valley are of a similar age and may have been initiated by European land clearance. A mosaic of tree ages is seen in Dennistoun Bush, and is seen to be a direct result of different aged flood surfaces. Dennistoun Bush 2 stand could have been initiated by the flood of circa 1740 AD (possibly initiated by the earthquake of 1748A.D.), and Dennistoun Bush 1 may have been initiated by a flood event 80 - 100 years earlier. The huge totara present in Dennistoun Bush may have been initiated by a flood event even earlier than the above recorded events. Tree ages in the present study concur with those found by Hall (1993), who used podocarp ages to determine surface age.

Figure 5.4 Absolute ages and disturbance chronologies for Okuti Valley and Dennistoun Bush.



5.3 DISCUSSION

In a general discussion on conifer regeneration in New Zealand, Ogden (1985) argues that a "gap-phase" or "mosaic" regeneration model is most appropriate for New Zealands canopy conifers. Ogden (1985) sees the regeneration of New Zealand conifers as resulting from both small and large-scale disturbance events, the interaction between the two often complicating interpretation of forest dynamics.

Windthrow has been proposed as one mechanism initiating podocarp regeneration in dense lowland podocarp forest (Shaw 1983, Ogden 1985) and is seen on scales appropriate for these podocarp forests. Regeneration is rare under a dense podocarp canopy but does occur beneath a gradually opening hardwood canopy (Beveridge 1973a). A sequential canopy collapse theory is proposed by Lusk (1989) for dense podocarp forest: elevated light levels due to canopy collapse allows the more light demanding species to enter. As the canopy re-closes species stop entering depending upon their shade tolerance. Periodic large scale disturbance re-initiates the regeneration of dense podocarps.

The terrace rimu forests of Westland exhibit a mosaic pattern of even-aged stands (see Norton et al 1988). Disturbance is seen as a major factor in the regeneration of these stands and for this reason seedlings and saplings of the canopy dominants are not expected to be present under a closed podocarp canopy. Several new Zealand studies show that rimu is able to maintain itself at a site with disturbance the main driving force. June (1982) observed that large rimu seedlings occurred on fallen, rotten logs and stumps, and on mounds resulting from the windthrow of several trees.

Lowland totara has long been considered a light demanding species (e.g. Cameron 1960a, McKelvey 1963) with a pioneer strategy colonising infertile or recently disturbed sites, perhaps under a nurse crop (e.g. Greenwood 1949, Beveridge 1983). There is strong evidence that lowland totara is unable to regenerate beneath a closed canopy or even in small gaps within the canopy. Its regeneration appears most vigorous in large windthrow gaps, forest margins or in open scrub and grassland (i.e. in high light or disturbed areas). If lowland totara is a light demanding species, canopy gaps would have to be very large to allow enough light to enter for totara to regenerate.

In a recent study on podocarp seedling growth rates under different light regimes Ebbett & Ogden (1998) elucidate seedling strategies. Lowland totara is shown to have high seedling growth rates in elevated light levels such as those found under catastrophic disturbance regimes which destroy the canopy. Matai is a consistent grower, slowly attaining the canopy through persistence and shade tolerance. Miro is intermediate in shade tolerance and captures sites such as canopy gaps created by medium-scale disturbance events such as wind-throw. Beveridge and Franklin (1977) report that rimu seedlings show high growth in small canopy gaps. Smale and Kimberley (1986) note that rimu and miro can survive and respond to canopy openings.

In the present study, likely disturbance regimes of each study site were identified. Regeneration was seen to occur in canopy gaps (Mananui), on flood surfaces (Dennistoun Bush, Coke Covenant, Price's Valley), following fire (Okuti Valley), and on prograding dunes (Nikau, Mananui). The active alluvial fan of Dennistoun Bush provides an insight into the effect of disturbance on forest composition.

The deposition of silt and gravel as a result of a flood event will affect the drainage regime and hence the distribution of kahikatea and totara. Massam (1986) documents the death of kahikatea trees adjacent to Dennistoun Bush as a result of gravel deposition from the 1975 flood event. Massam (1986) considers this damage to be significantly affecting the long term survival of kahikatea on this site. The regeneration of kahikatea on alluvial fans following silt deposition is well documented (e.g. Wardle 1974) but it may be that gravel deposition will adversely effect kahikatea regeneration due to its effect on drainage status. The importance of flood events and subsequent silt and gravel deposition for the regeneration of totara, matai, and kahikatea forests is also documented for Westland (Foweraker 1929, Wardle 1974, McSweeney 1982, Duncan 1993).

The ability of totara and kahikatea to respond to elevated light levels (Ebbett & Odgen 1998) indicates the importance of disturbance in the regeneration of lowland totara. Lowland totara is seen to actively colonise new surfaces such as coastal dunes. Catastrophic disturbance such as fire, landslip, and flood, act to remove the existing vegetation and expose new colonisation surfaces for lowland totara domiated forest. Medium levels of disturbance such as windthrow create canopy gaps with elevated light levels, allowing totara and kahikatea to regenerate. Disturbance regimes favouring the regeneration of totara dominated stands therefore appears to be in the medium to catastrophic range.

Plate 8 Active river plain where stands Coke Covenant 1 and 2 occur. Aorere River, Collingwood, Golden Bay.

Plate 9 Gravel deposition and flood damage from Kowhai Stream in Dennistoun Bush, 1986 (A) and 1993 (B). Peel Forest Park, Canterbury.

A

B

CHAPTER SIX
STAND DESCRIPTIONS

6.1 INTRODUCTION AND OBJECTIVES

In this chapter, stand descriptions of the sixteen study plots at the ten main study sites are presented. The relative abundance of each species is discussed and forest types assigned. Size and age class frequency distributions are presented, as well as profile diagrams showing vertical forest structure.

The objectives of this chapter are:
- To determine what forest types occur and to determine if previous classifications are adequate in describing lowland totara forest types
- To describe the structure of lowland totara forest in terms of number, basal area, and species composition
- To describe the vertical structure of lowland totara forest
- To investigate the age structure of the stands

6.2 STUDY SITE FOREST TYPES

6.2.1 Methods

Forest types are assigned on the basis of adult stems per hectare, with fifteen percent composition used as the arbitrary dividing line. For example, sites with 75% totara and 25% matai are classified as totara/matai, sites with 70% totara, 15% matai, and 15% kahikatea are classified as totara/matai/kahikatea. Pure totara is classified as having greater than 85% (total adult stems per hectare) totara. When percent basal area is used to define forest type, more stands become classified as pure totara and less as almost pure matai.

6.2.2 Results

Figure 6.1 outlines the species composition of the study plots based on number of adult podocarp stems per hectare (A) and basal area of podocarp saplings and

adults (B). Only sites where lowland totara, matai, and kahikatea represent more than 95% of the total stems per hectare or basal area of the podocarps present in a plot are included. Nikau, Mananui, and Blue 2 are excluded as they contain significant proportions of rimu and/or miro and so are classified as dense mixed stands. Percent rimu and/or miro ranges from 23% in Blue 2, to 16% in Mananui, to 12% in Nikau.

Forest types identified from Figure 6.1A (number per hectare) are used throughout this thesis and range from pure totara, to almost pure matai, to totara - matai, to totara - kahikatea, to a combination of totara - matai - kahikatea, to dense mixed podocarps (more than 5% of the adult podocarp stems per hectare). Forest types generally agree with the classification of Nicholls (1976) and McKelvey (1984) except for the gradation seen between the totara/matai and totara/kahikatea classes. In the present study gradations from totara/matai, to totara/kahikatea, to totara/matai/kahikatea were observed. The percent composition of totara, matai, and kahikatea may well be dependent upon soil and drainage conditions, as well as seed source and disturbance regime. Plate 11 shows a large kahikatea in Price's Valley Covenant, an almost pure matai stand.

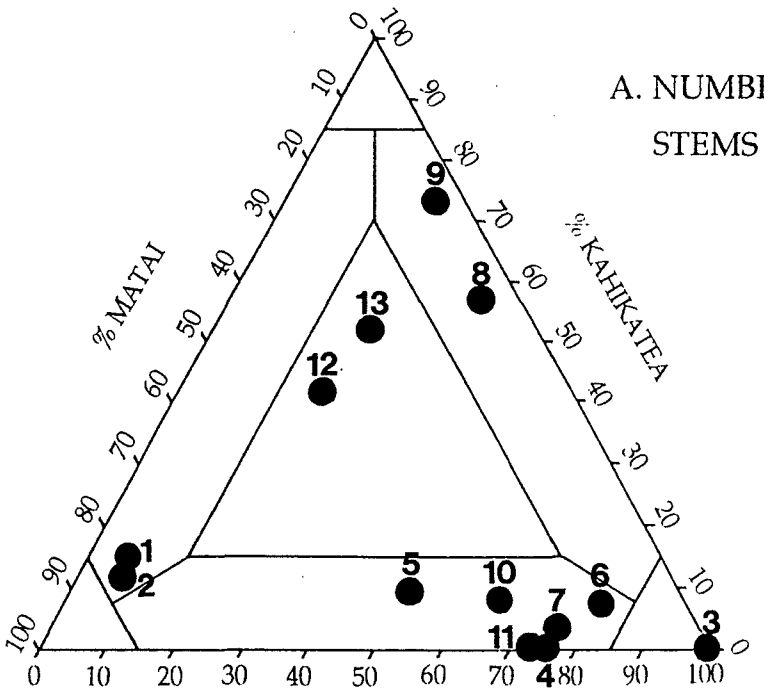
Basal area (m^2 per hectare) at all sites is presented in Figure 6.2. Figure 6.2A shows total podocarp and angiosperm basal area per hectare for all sites. In general, basal area increases from young/developing stands through to mature and senescent stands. Basal area does not appear to be additive i.e. an increase in podocarp basal area is not accompanied by a corresponding significant decrease in angiosperm basal area. Angiosperm basal area fluctuates throughout the sites around a mean value of approximately $20m^2$.

Figure 6.2B shows basal area (m^2 per hectare) for all species at all sites. Study sites are arranged from pure totara, to totara/matai, to almost pure matai, to gradations of totara/matai/kahikatea, to dense mixed podocarps. Basal area is somewhat correlated with development status; young/colonising stands have the least basal area, mature and senescent stands have the greatest basal area. Basal area however, appears to be correlated with forest type; pure totara and totara/matai stands have the least basal area, totara/matai/kahikatea have the greatest basal area.

Pure matai and pure kahikatea stands were not encountered in the present study, possibly because the target species was lowland totara. However, in the almost pure matai stands of Puhi Puhi (82% of adult stems are matai) and Price's Valley (81% of adult stems are matai) occasional totara and kahikatea occur.

Figure 6.1 Study site stand associations based on percent podocarp composition. A. Number of adult stems per hectare, B. Basal area per hectare. See text for explanation.

A. NUMBER OF ADULT STEMS PER HECTARE.



KEY
1. Price's Valley
2. Puhi Puhi
3. Payne's Ford
4. Okuti Valley
5. Okuti kanuka
6. Coke Covenant 1
7. Coke Covenant 2
8. Denn Bush 2
9. Denn Bush 1
10. Blue Duck 1
11. Peraki Saddle
12. Big Tree
13. Denn Huge

B. BASAL AREA PER HECTARE.

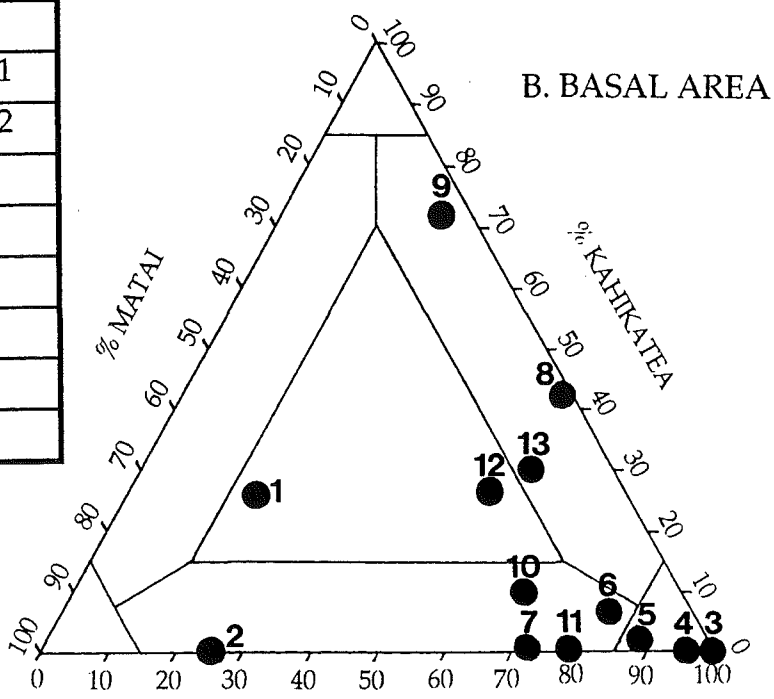


Figure 6.2A Total podocarp and angiosperm basal area at all sites.

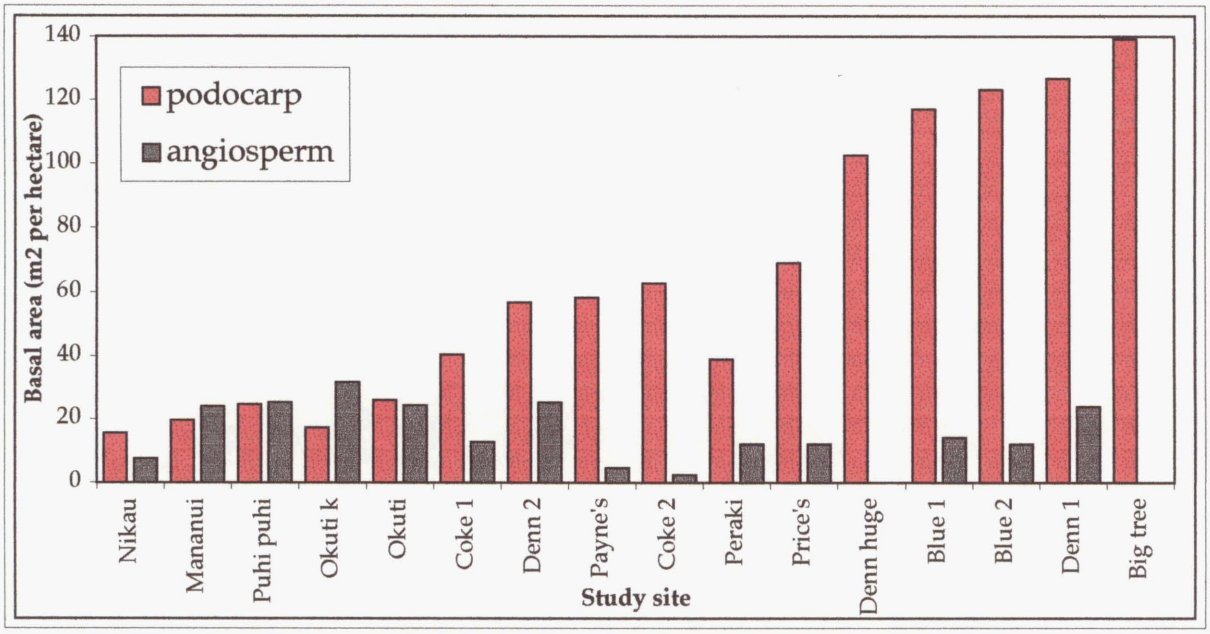
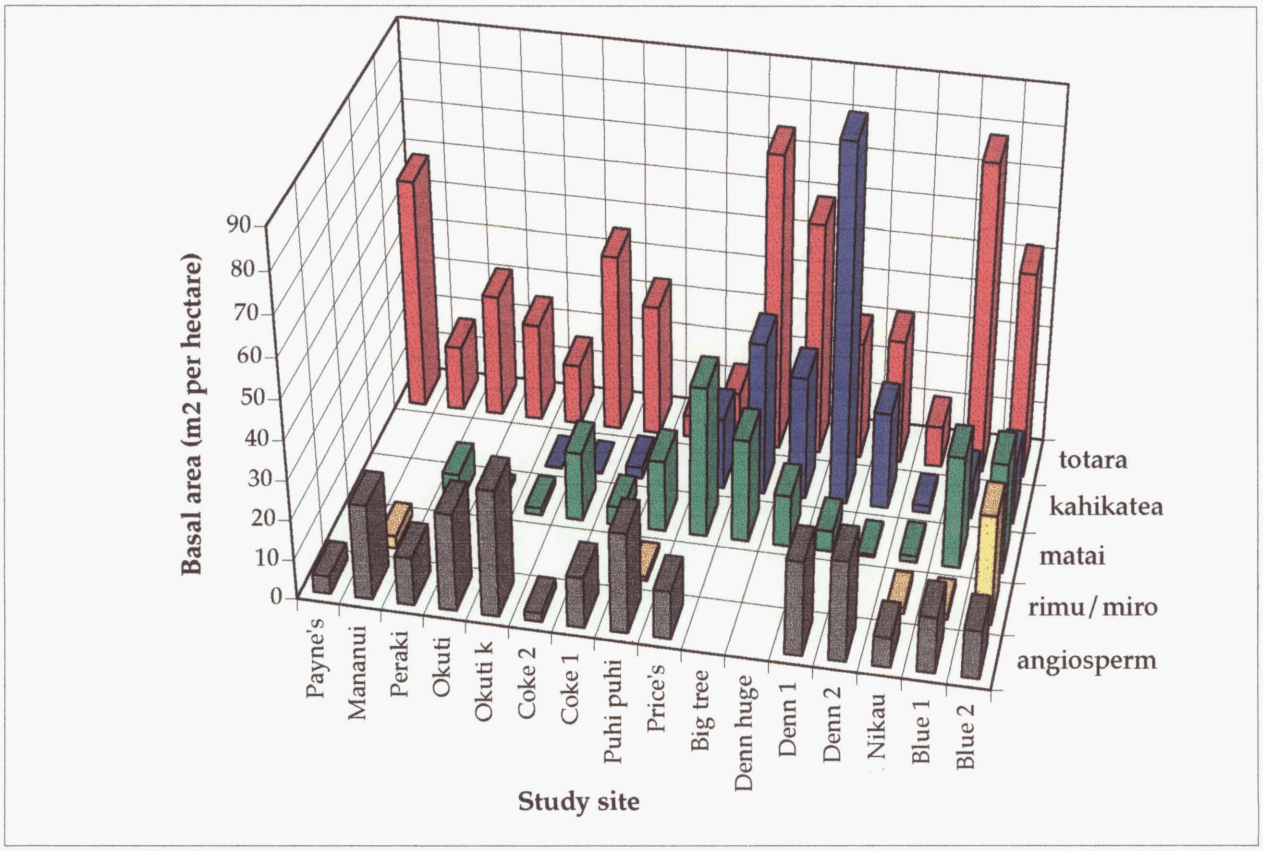


Figure 6.2B Basal area per hectare for all species (including angiosperms) at all sites.



A note on hybrids

While an effort was made to restrict sampling to lowland totara dominated stands, three of the study plots contained *Podocarpus* hybrids. Mananui Bush Scenic Reserve is located on the distributional boundary between *P.totara* and *P.totara* var. *waihoensis* and the totara trees present have affinities with both parents i.e. individuals have variable bark, leaf form, and height. For this reason these individuals are classified as a hybrid between both parents (identification confirmed by Brian Molloy).

Two study plots (Nikau Scenic Reserve, Westland, and Peraki Saddle Scenic Reserve, Banks Peninsula) contain hybrids between *P.totara* and *P.hallii*. Plate 12 shows seedlings of *P.totara* and *P.hallii* growing adjacently in Nikau Scenic Reserve, Westland. Table 6.1 shows the number of *Podocarpus* hybrids at these two sites, the general ratio of parent to second parent to hybrid being 7:2:1.

Table 6.1 *Podocarpus* parent and hybrid numbers at Peraki Saddle and Nikau Scenic Reserves.

STUDY SITE	Altitude (m.a.s.l.)	Total number	*P.totara*		*P.hallii*		*tot x hallii*	
			n	(%)	n	(%)	n	(%)
Peraki Saddle S.R.	400 - 460	25	5	(20)	17	(68)	3	(12)
Nikau S.R.	0 - 5	57	40	(70)	10	(17.5)	7	(12.5)

It is interesting to note that the percentage of hybrids is relatively constant and appears to be independant of altitude or the percentage of parents present at a site. The percentage of parents at a site appears to be a function of altitude; *P.totara* is replaced in dominance by P.*hallii* at altitudes above 400-500m. It has been suggested that on Banks Peninsula three forms of *Podocarpus* occur; *P.totara* in lowland regions, *P.hallii* above 400m and a stable hybrid between the two which is shorter in stature than *P.totara* and has the thin bark of *P.hallii* (Hugh Wilson pers.comm.). Peraki Saddle Scenic Reserve spans this altitudinal boundary, hence the occurrence of all three types.

6.3 STAND DESCRIPTIONS

6.3.1 methods

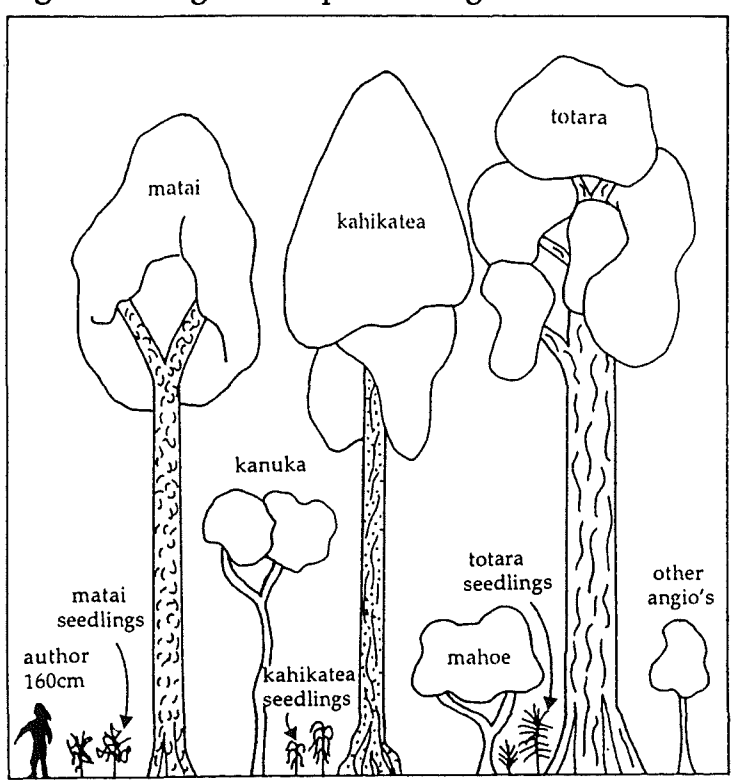
The following descriptions present size class frequency distribution and profile diagrams for all stands. Profile diagrams are all drawn to scale and represent 10 x 30m strips (except Puhi Puhi which is only 20m long) taken off study site plot maps and combined with height values recorded in the field (data collection methods described in section 3.3.2). Crown widths are estimated from canopy position and condition, and plot map locations i.e. trees in a continuous canopy would be expected to have similar sized crowns based on tree spacing.

Size class frequency graphs are divided into 10cm size classes except for the first size class of the saplings, which are defined as 5-9.9cm DBH. Four major development categories are recognised and will be used consistently throughout this thesis (see section 3.2.2), and appear below in the following order: young/colonising stands, developing stands, mature stands, and senescent stands.

6.3.2 Results

The legend for the profile diagrams appears below (Fig.6.3).

Figure 6.3 Legend for profile diagrams.



Young/colonising stands

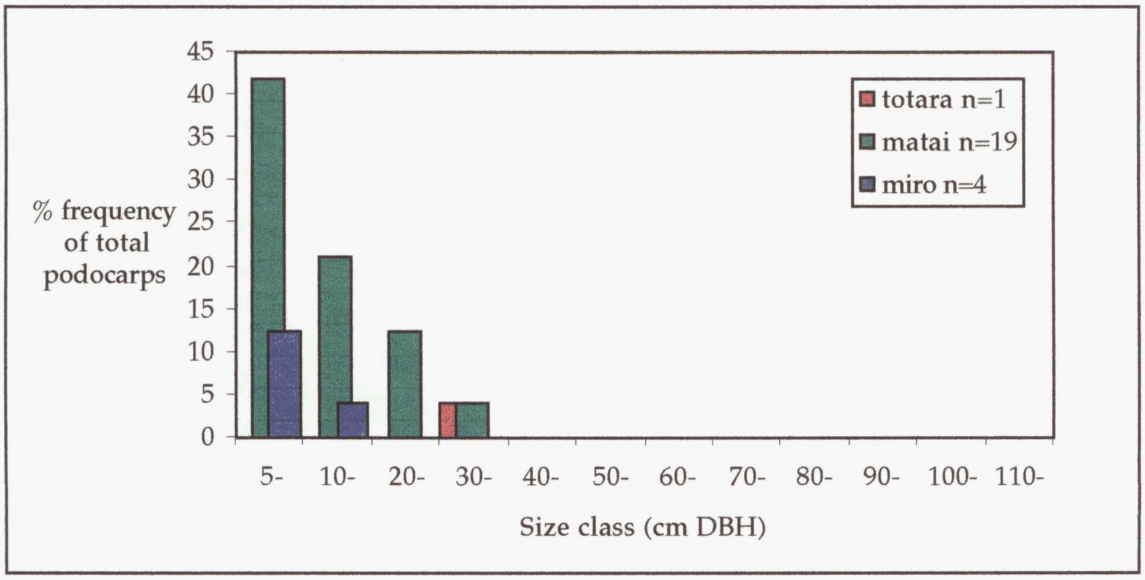
• Puhi Puhi Scenic Reserve (Fig. 6.4). This stand is colonising an active alluvial river terrace with young yellow brown earth soils. Forest type is classified as pure matai. Dense matai seedlings occur under emergent angiosperms. Several small matai occur (less than 40cm DBH) and only one totara adult.

• Mananui Bush Scenic Reserve (Fig. 6.5). This stand is colonising forward on an active sand dune system (see Plate 6). Soils are young yellow brown sands which are highly leached due to the high rainfall of the area (circa 2700mm per annum). Forest type is classified as dense mixed podocarp although lowland totara is the dominant species. Seedlings, saplings, and adults of rimu and rarely miro also occur. Canopy is closed due to wind exposure. Totara seedlings and saplings are common under angiosperms and in canopy gaps. All podocarps are less than 100cm DBH.

• Nikau Scenic Reserve (Fig. 6.6). This stand is colonising gravel dunes which have yet to develop a definite soil structure (see Plate 6). Rainfall is also high (circa 2400mm per annum) although drainage is unimpeded due to the gravel substrate. Forest type is classified as dense mixed podocarp as all of the five main podocarps occur, as well as Hall's totara and hybrids with lowland totara. Canopy is mostly closed due to wind exposure although canopy gaps "full" of seedlings occur. All podocarps are under 70cm DBH.

Figure 6.4 Puhi Puhi Scenic Reserve stand description.

A. Size class frequency distribution.



B. Profile diagram.

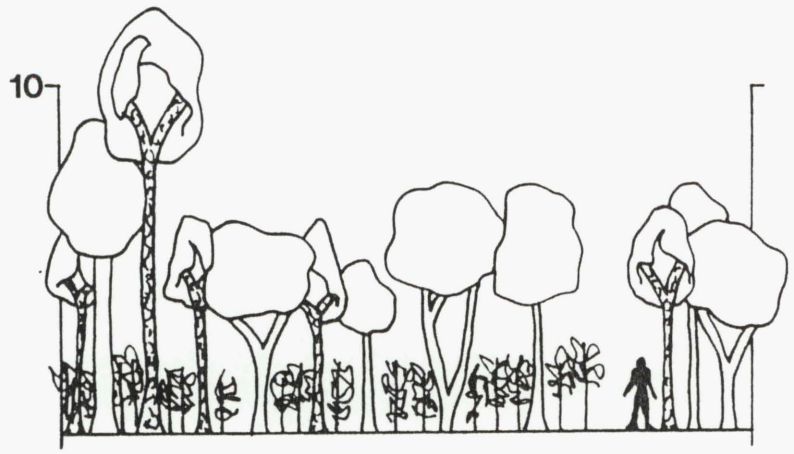
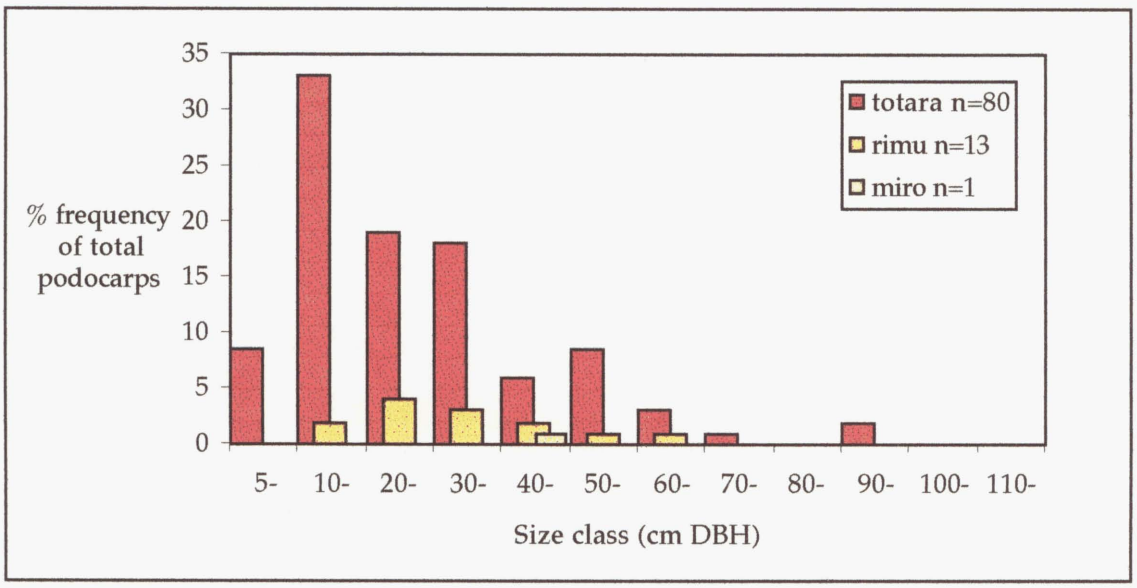


Figure 6.5 Mananui Bush Scenic Reserve stand description.

A. Size class frequency distribution.



B. Profile diagram.

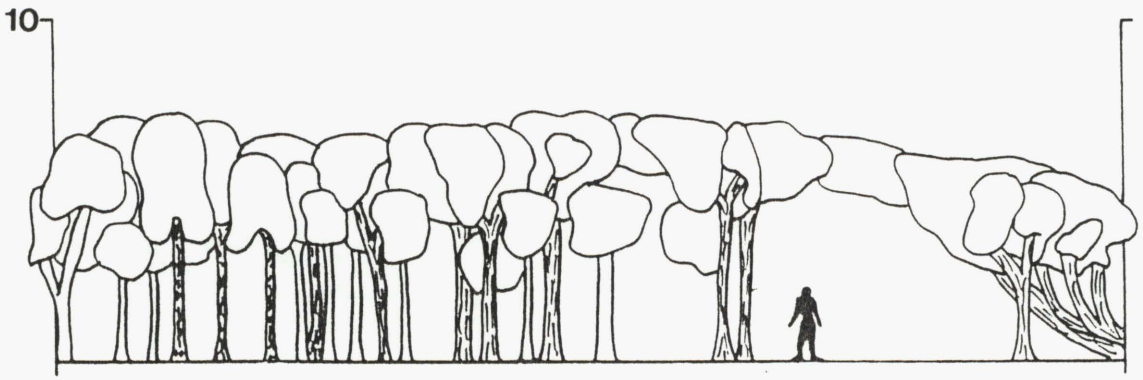
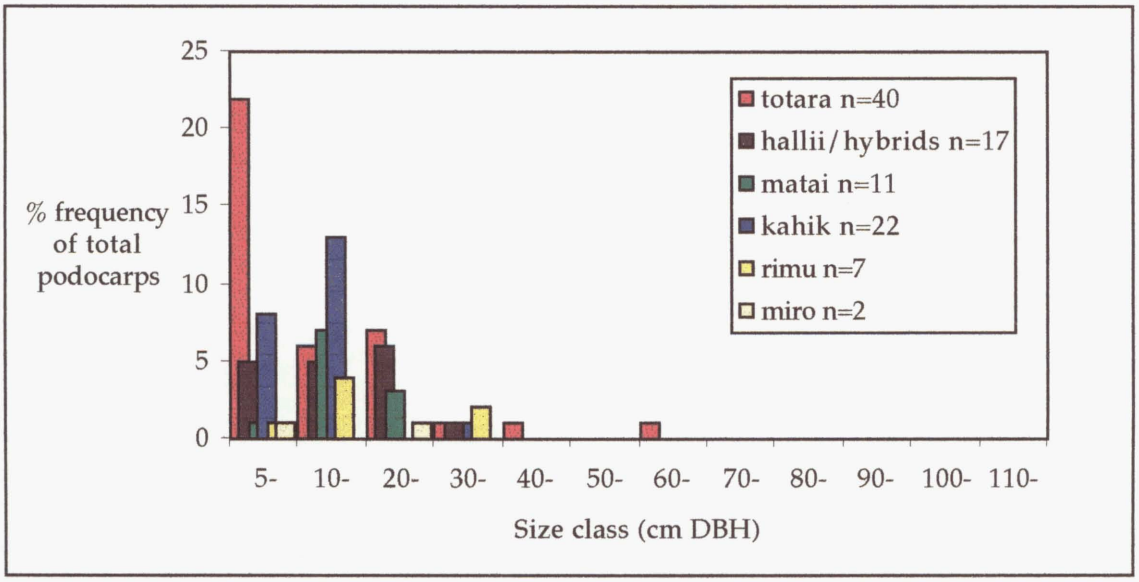
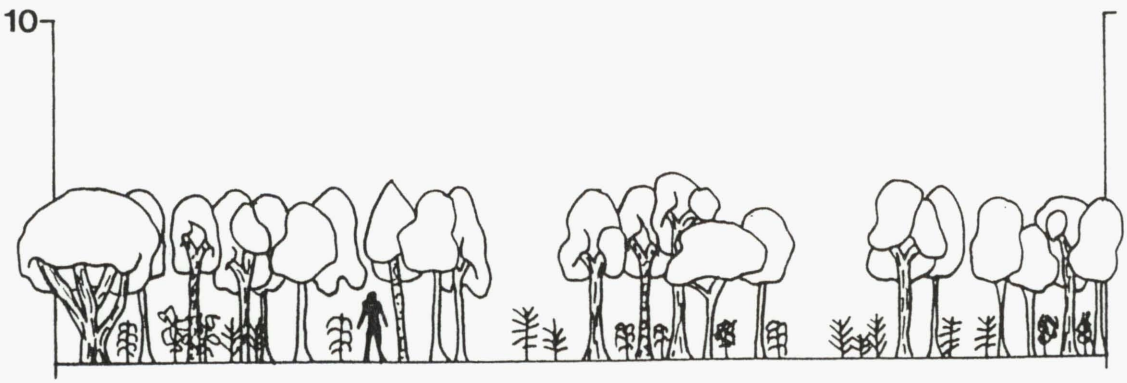


Figure 6.6 Nikau Scenic Reserve stand description.

A. Size class frequency distribution.



B. Profile diagram.



Developing stands

• Payne's Ford Scenic Reserve (Fig. 6.7). This stand occurs on a rocky outcrop with rendzina soils adjacent to a limestone bluff. Two emergent lowland totara seed trees are present (see Plate 13) as well as younger individuals which form a sparse canopy. The forest type is pure totara although one matai seedling was encountered.

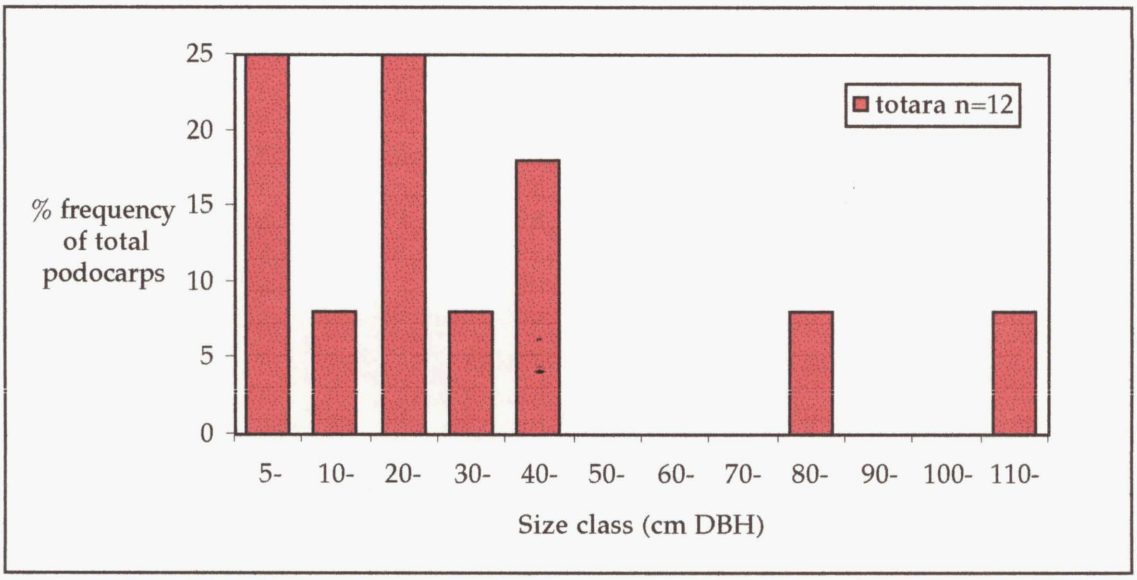
• Coke Covenant 1 (Fig. 6.8).
• Coke Covenant 2 (Fig. 6.9). The Coke Covenant stands occur on an active river delta and are separated by a river course (see Plate 8). Soil is mostly fertile river sand and is classified as recent. Forest type is classified as totara - matai in both stands although varying amounts of kahikatea occur. Canopies are continuous and closed, several saplings and seedlings occur. In both plots podocarps are under 90cm DBH.

• Okuti Valley Scenic Reserve (Fig. 6.10).
• Okuti Valley Scenic Reserve kanuka (Fig. 6.11). Both of these stands occur on an old river terrace or landslip site. Soil is fertile yellow brown earths. Both are classified as totara - matai although Okuti (kanuka) has a significant proportion of senescent kanuka which form a subcanopy under emergent totara and matai. A few kahikatea individuals occur around the general area but are restricted to waterlogged depressions. Okuti canopy consists of an angiosperm subcanopy under emergent totara and matai (see Plate 2). Seedlings and saplings are common. All podocarps are under 80cm DBH.

• Dennistoun Bush Scenic Reserve 2 (Fig. 6.12). This stand occurs on an active alluvial fan upon which flood events have deposited silt and gravel (see section 5.3.4., plates 9 and 10). Soils are fertile yellow brown earths. Forest type is classified as totara - kahikatea, although matai saplings do occur. The podocarp canopy is nearly continuous with an angiosperm understorey. Seedlings and saplings are common. Podocarps are all under 80cm DBH.

Figure 6.7 Payne's Ford Scenic Reserve stand description.

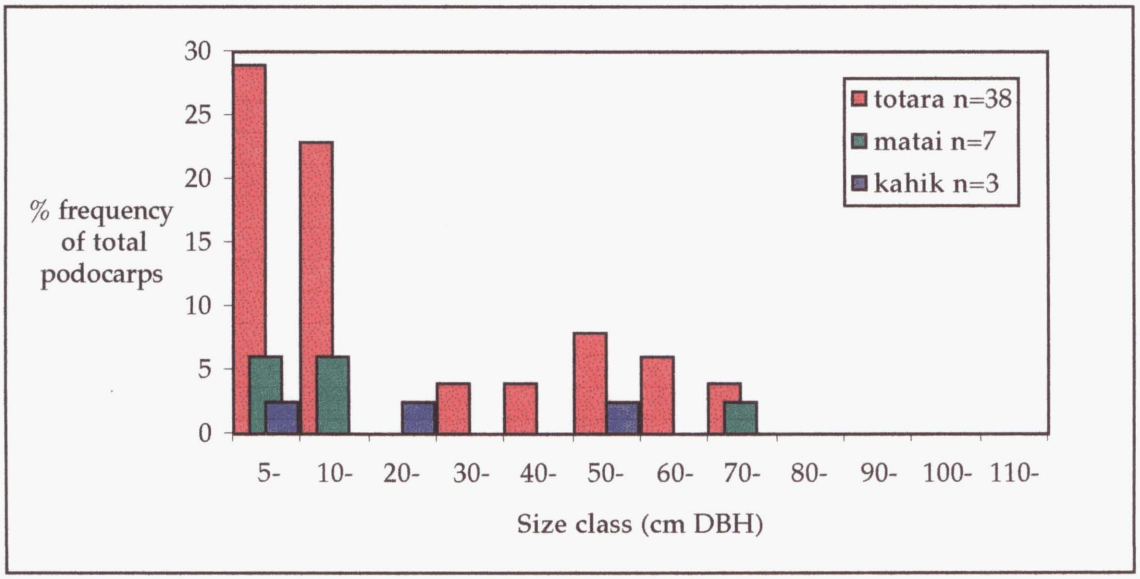
A. Size class frequency distribution.



B. Profile diagram.

Figure 6.8 Coke Covenant 1 stand description.

A. Size class frequency distribution.



B. Profile diagram.

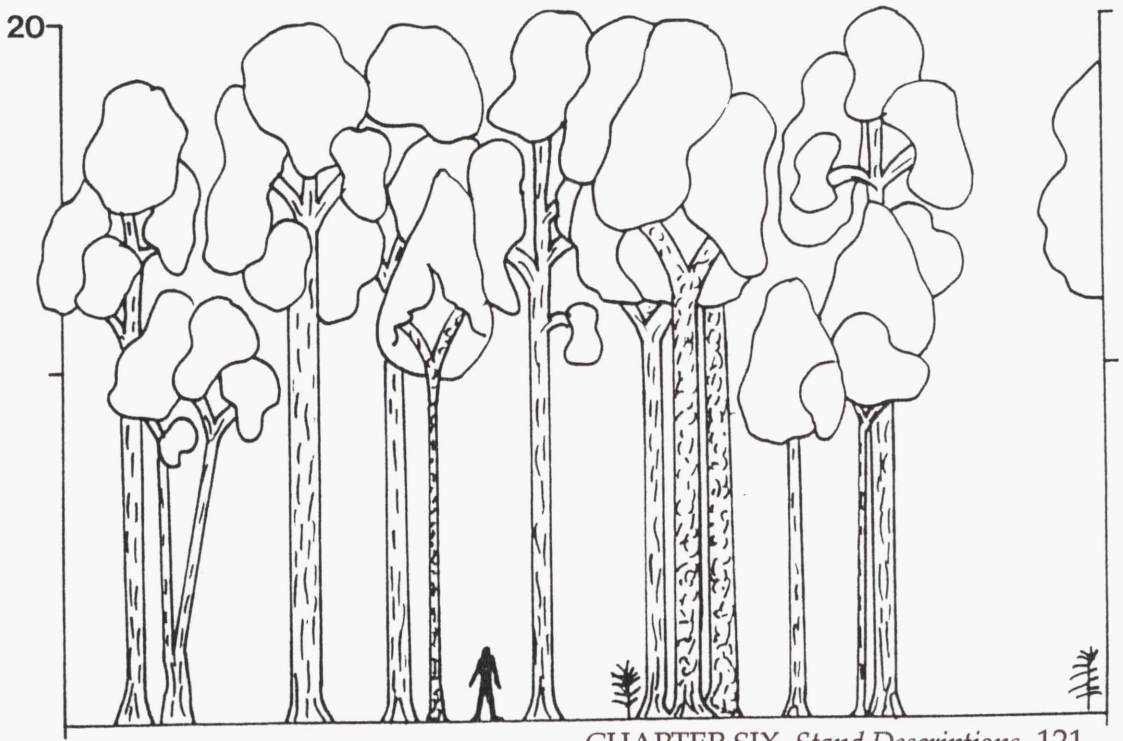
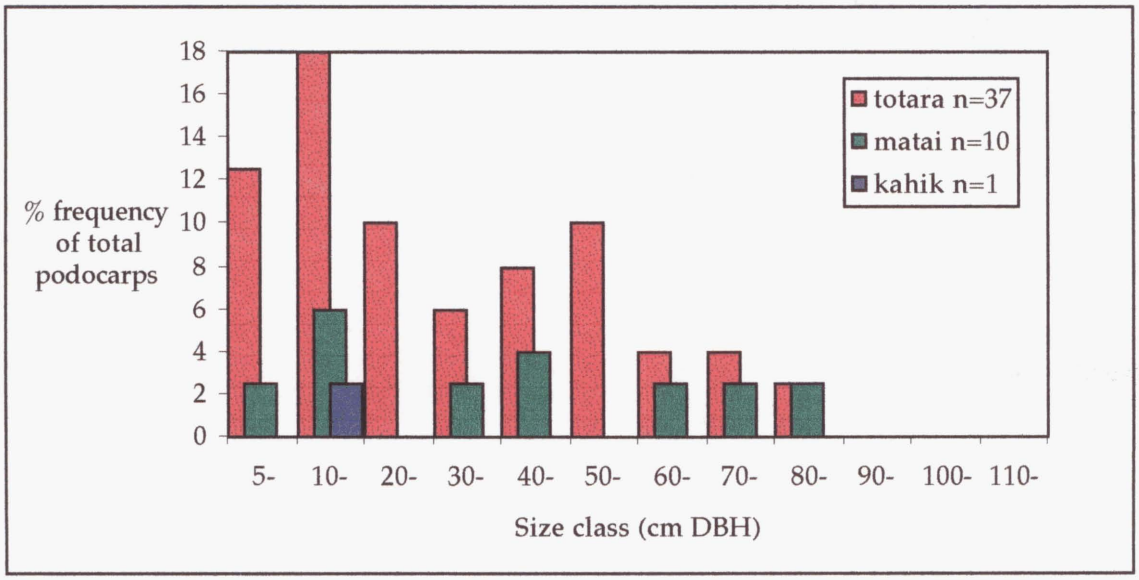


Figure 6.9 Coke Covenant 2 stand description.

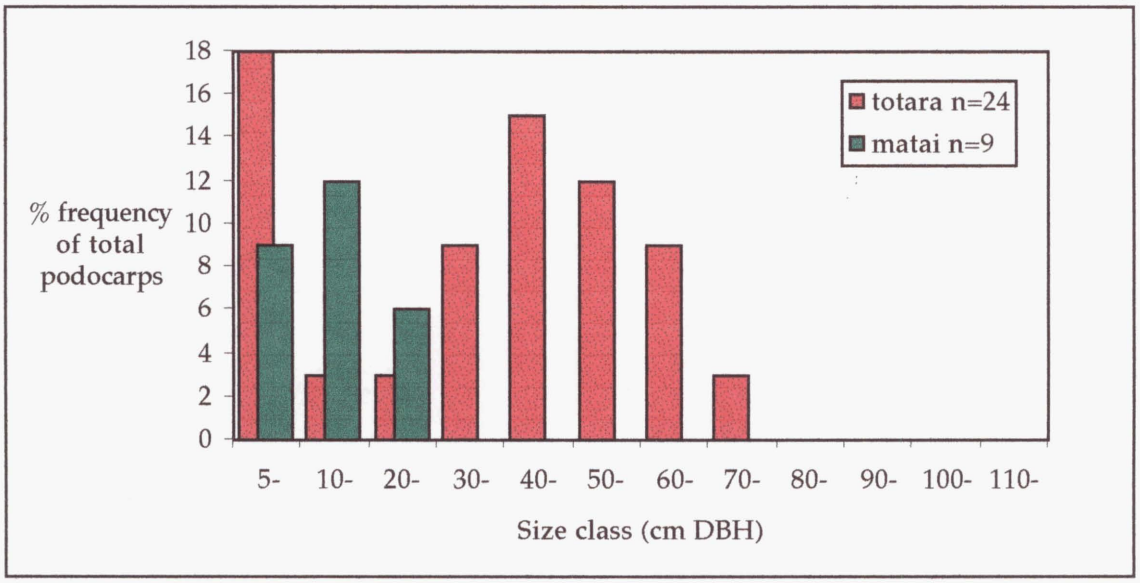
A. Size class frequency distribution.



B. Profile diagram.

Figure 6.10 Okuti Valley Scenic Reserve stand description.

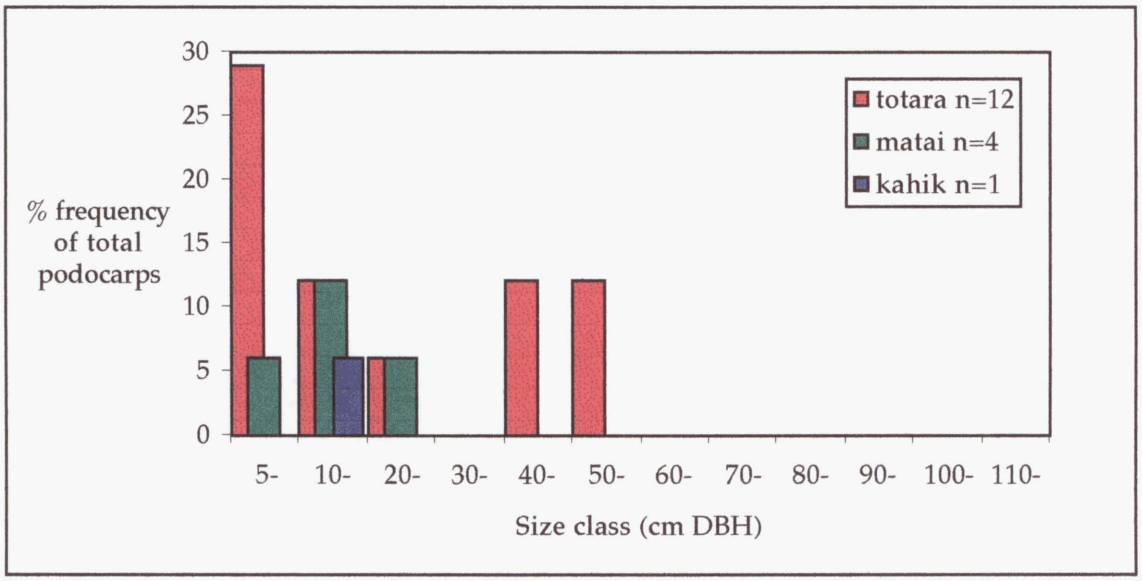
A. Size class frequency distribution.



B. Profile diagram.

Figure 6.11 Okuti Valley Scenic Reserve (kanuka) stand description.

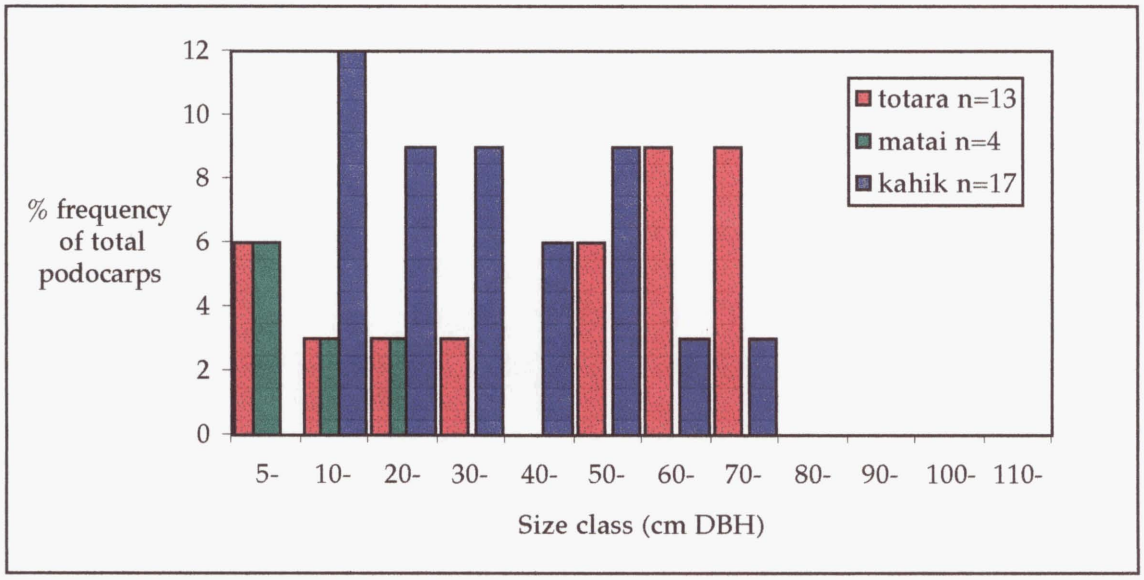
A. Size class frequency distribution.



B. Profile diagram.

Figure 6.12 Dennistoun Bush Scenic Reserve 2 stand description.

A. Size class frequency distribution.



B. Profile diagram.

Mature stands

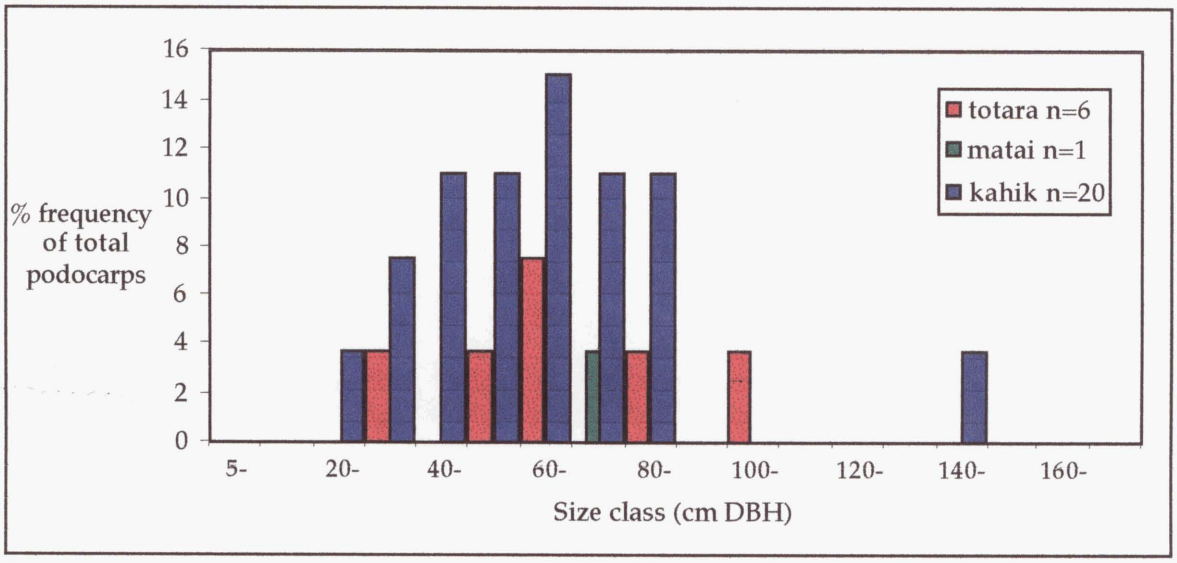
• Dennistoun Bush Scenic Reserve 1 (Fig. 6.13). This stand occurs on the same active alluvial fan as Denn Bush 2. Forest type is classified as totara - kahikatea although more kahikatea occurs than in Denn Bush 1. Canopy is continuous podocarps of 20 - 150cm DBH. Seedlings and saplings are rare.
• Price's Valley Covenant (Fig. 6.14). This stand occurs on a river plain and soils are recent. Forest type is classified as almost pure matai although a few totara and kahikatea individuals occur (see Plates 1, 4, and 11). Canopy is continuous with an understorey of titoki. Seedlings and sapling occur under angiosperms. Adult podocarps range from 40 - 170cm DBH.
• Peraki Saddle Scenic Reserve (Fig. 6.15). This stand occurs on a colluvial slope with brown granular loam hill soils (see Plates 7 and 15). Forest type is classified as totara - matai. Lowland totara occurs in the lower region and is replaced by Hall's totara above 450m. Intermediate between the two occurs a hybrid form. Several emergent trees have joined to formed areas of continuous canopy. Seedlings and saplings are rare. Diameter of the podocarps ranges from 10 - 180cm DBH, with the largest individuals being lowland totara.
• Blue Duck Scenic Reserve 1 (Fig. 6.16).
• Blue Duck Scenic Reserve 2 (Fig. 6.17). Both of these plots occur on colluvial slopes with yellow brown earth soils (see Plate 7) although Blue Duck 2 is in a ridge position and Blue Duck 1 on slope face. Forest type is classified as dense mixed in Blue Duck 2 as several rimu occur. Blue 1 is classified as totara - matai - kahikatea. Canopies are more or less continuous emergent podocarps over an angiosperm understorey. Seedlings and saplings are rare. Adult podocarp diameters range from 20 - 140cm DBH.
• Big Tree Peel Forest (Fig. 6.18). This stand occurs on a river terrace with yellow brown earth soils. Forest type is classified as totara - matai - kahikatea. Seedlings and saplings are rare. Canopy is more or less continuous emergent podocarps of 40 - 230cm DBH.

Senescent stands

• Dennistoun Bush Huge (Fig. 6.19). This stand also occurs on the Dennistoun Bush alluvial fan. Trees are all large (over 80cm DBH) and seedlings and saplings are rare. Forest type is classified as totara - matai - kahikatea and the canopy is continuous emergent podocarps with a sparse angiosperm understorey.

Figure 6.13 Dennistoun Bush Scenic Reserve 1 stand description.

A. Size class frequency distribution.



B. Profile diagram.

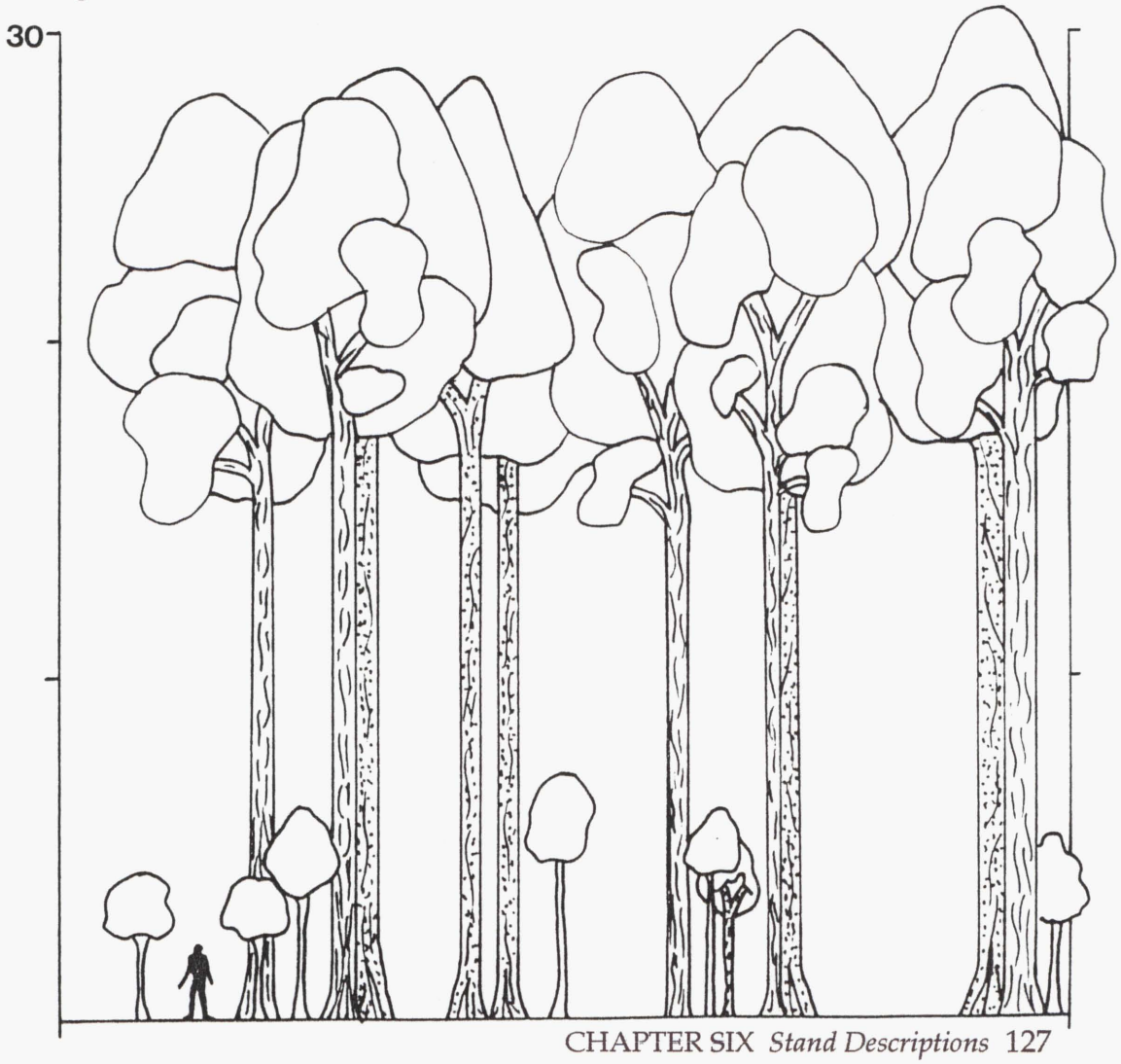
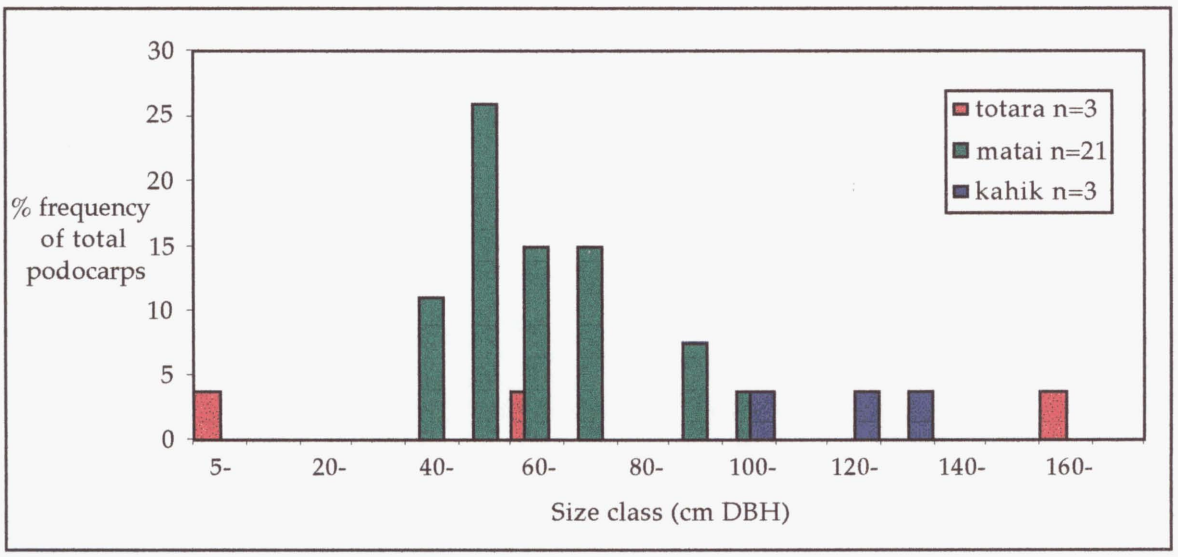


Figure 6.14 Price's Valley Covenant stand description.

A. Size class frequency distribution.



B. Profile diagram.

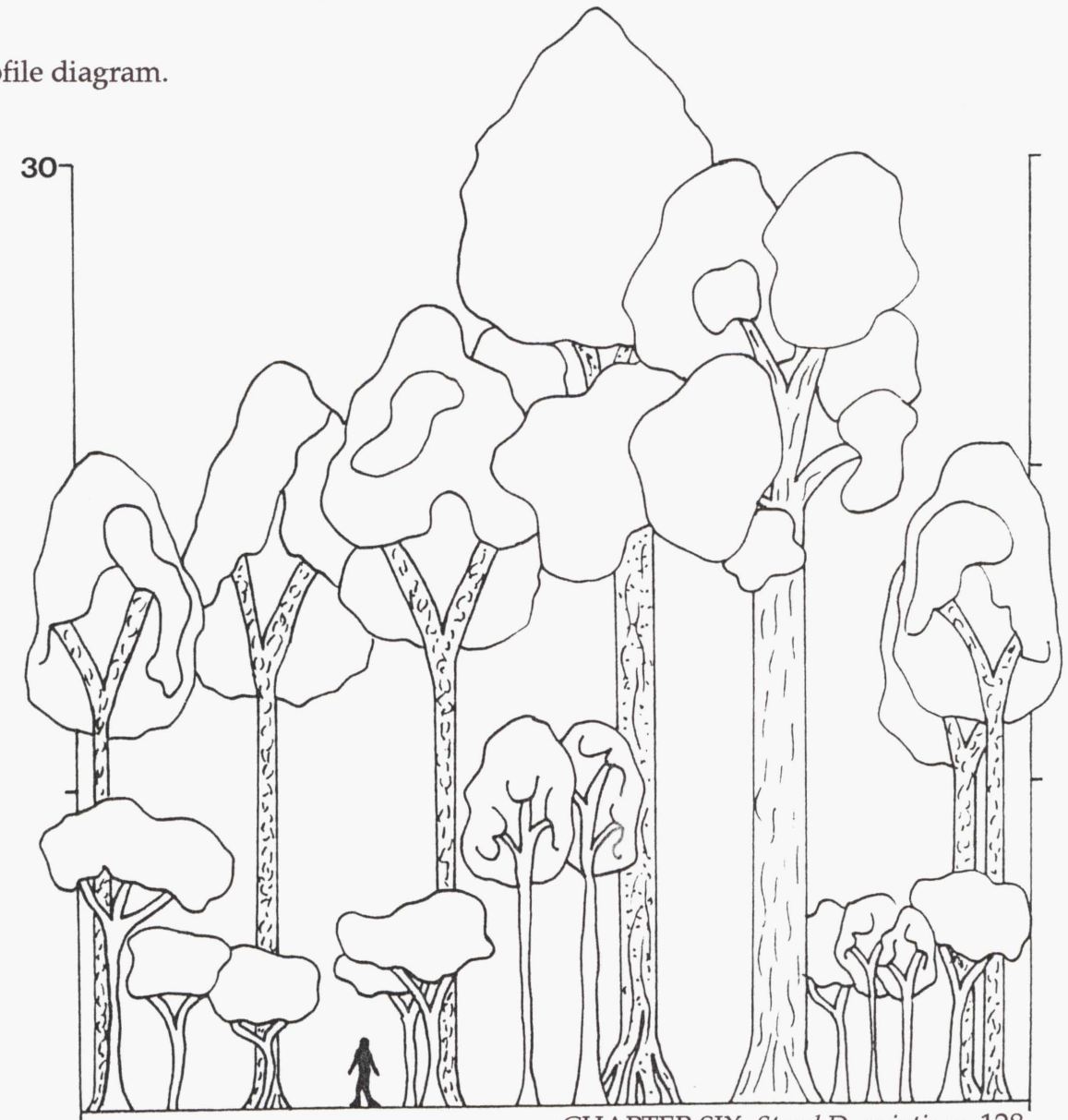
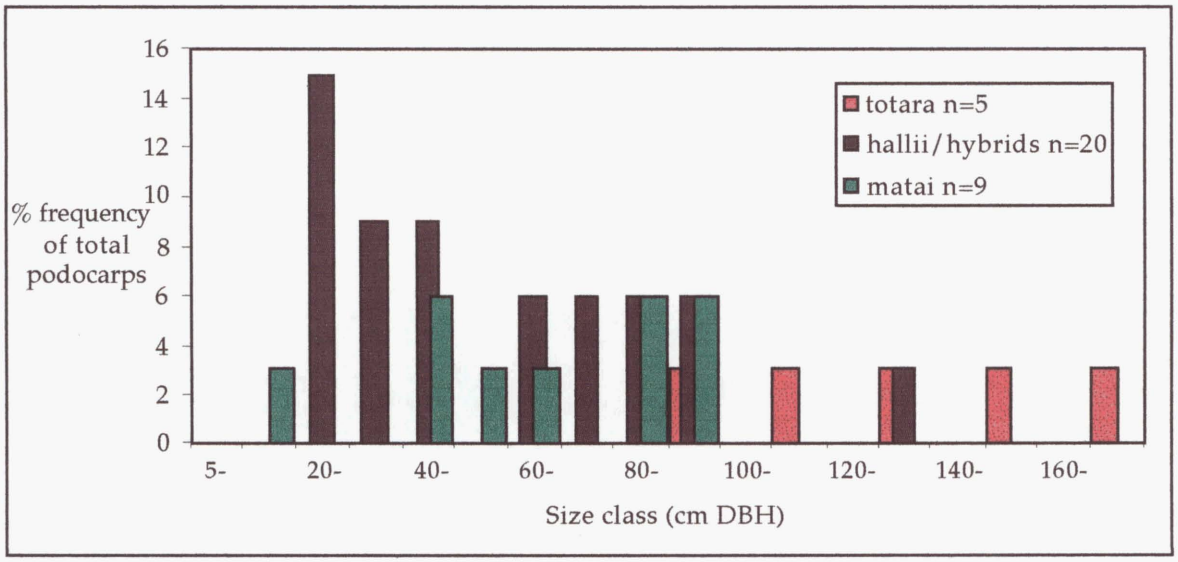


Figure 6.15 Peraki Saddle Scenic Reserve stand description.

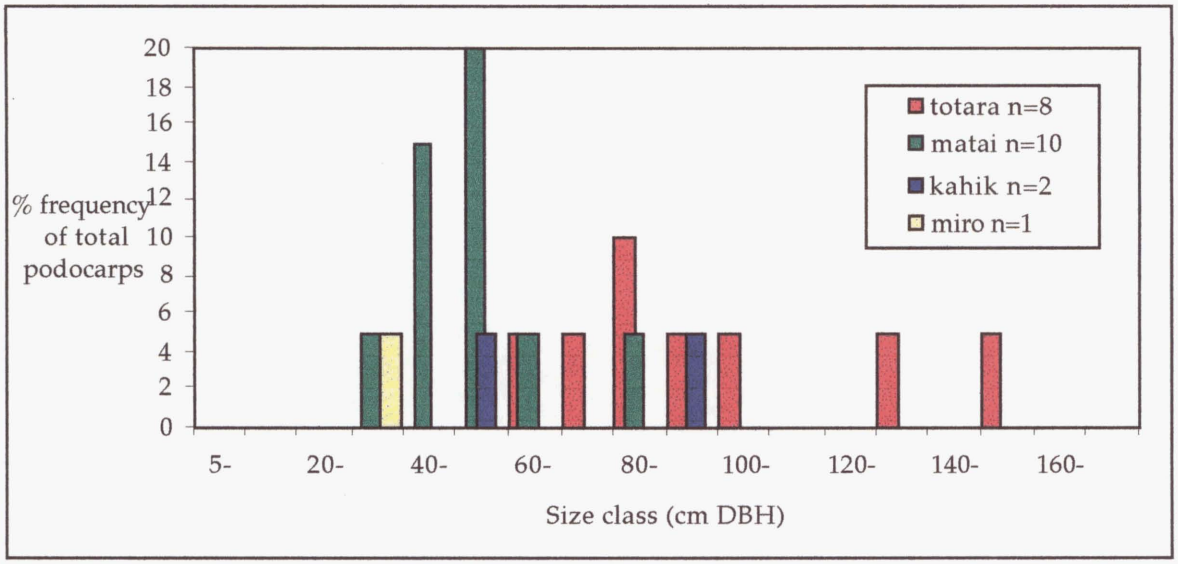
A. Size class frequency distribution.



B. Profile diagram.

Figure 6.16 Blue Duck Scenic Reserve 1 stand description.

A. Size class frequency distribution.



B. Profile diagram.

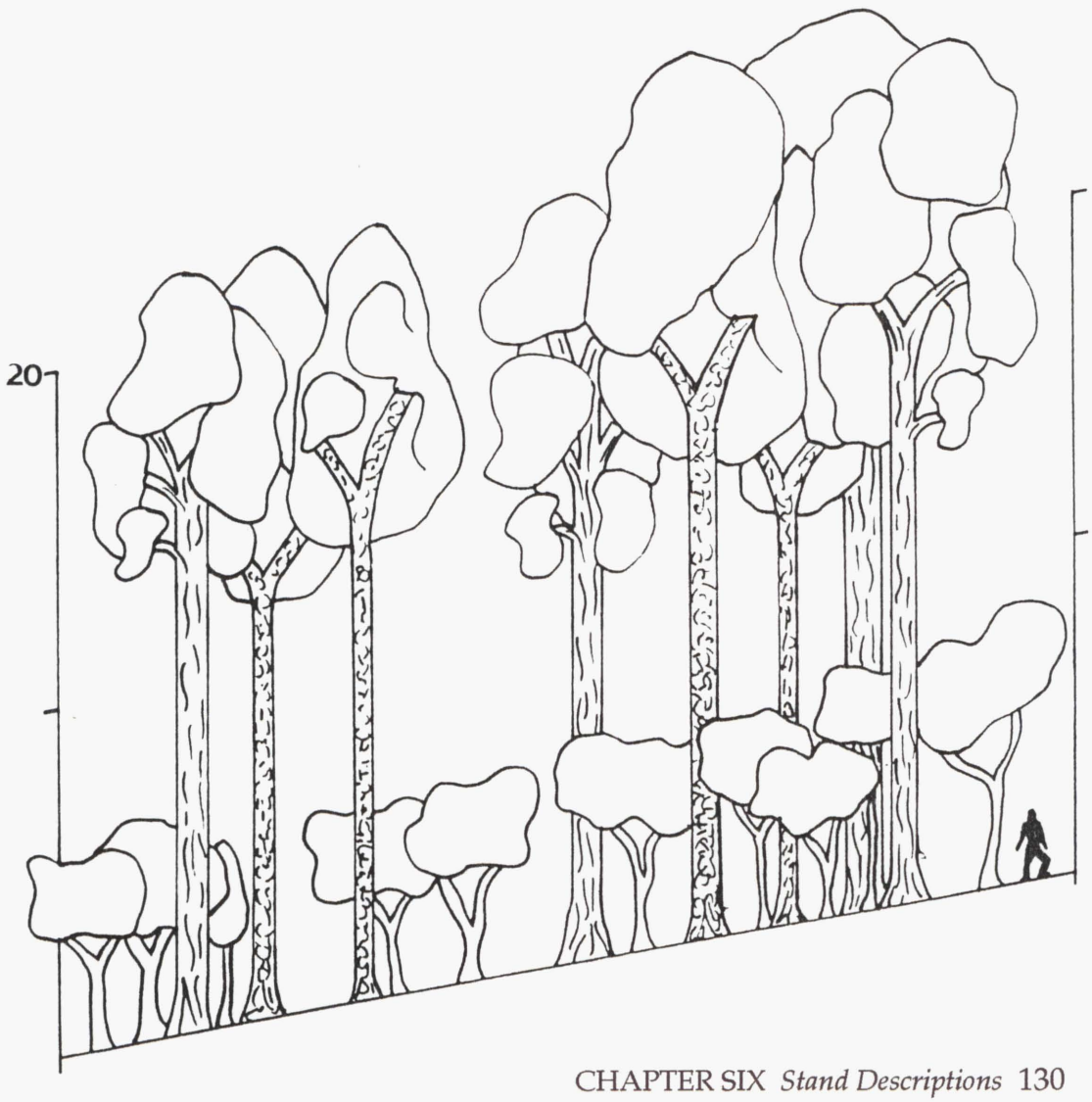
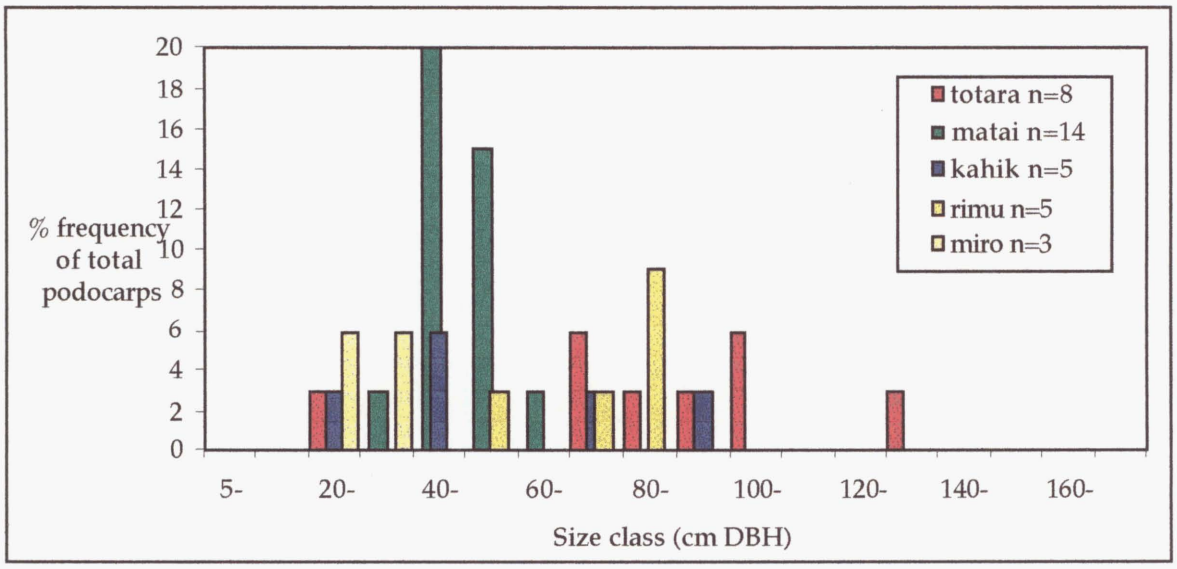


Figure 6.17 Blue Duck Scenic Reserve 2 stand description.

A. Size class frequency distribution.



B. Profile diagram.

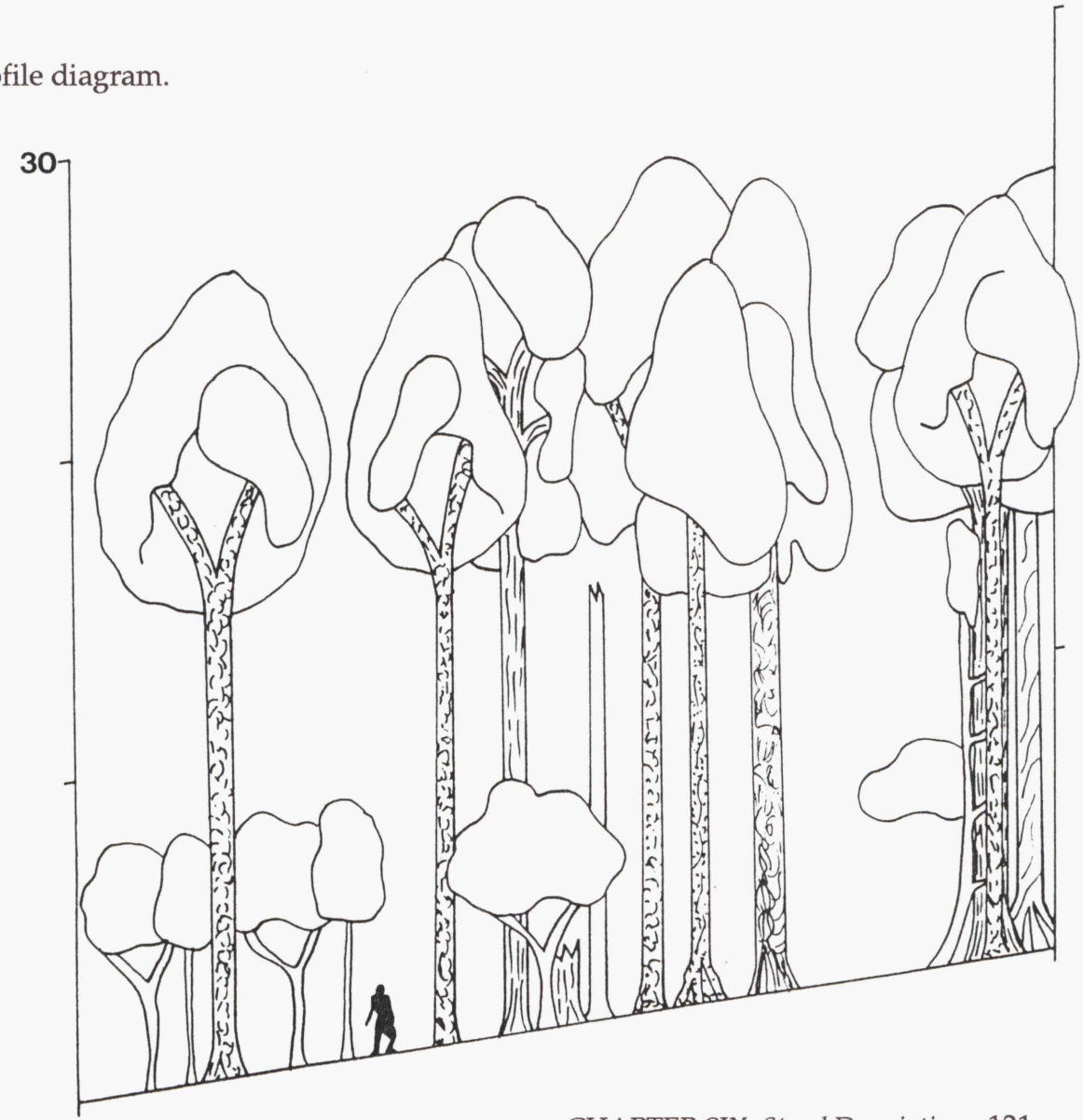
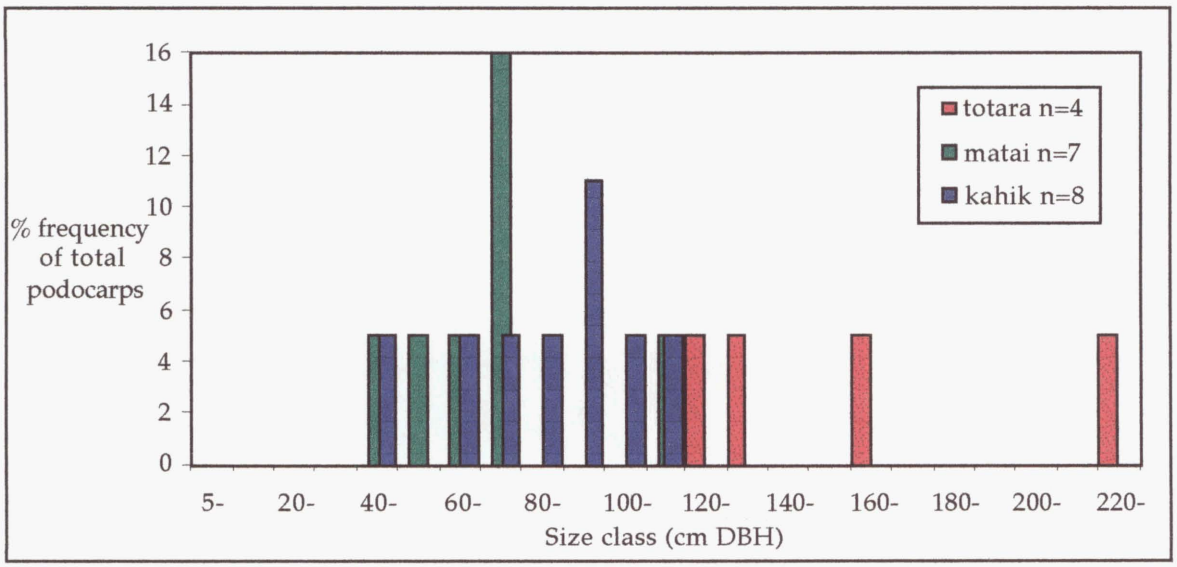


Figure 6.18 Big Tree Peel Forest stand description.

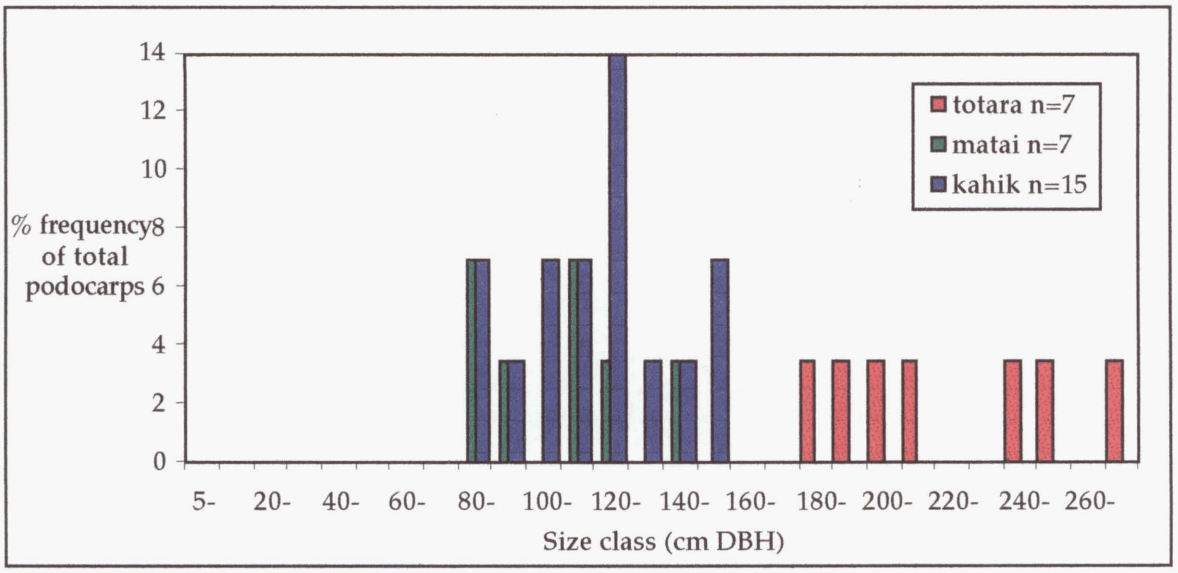
A. Size class frequency distribution.



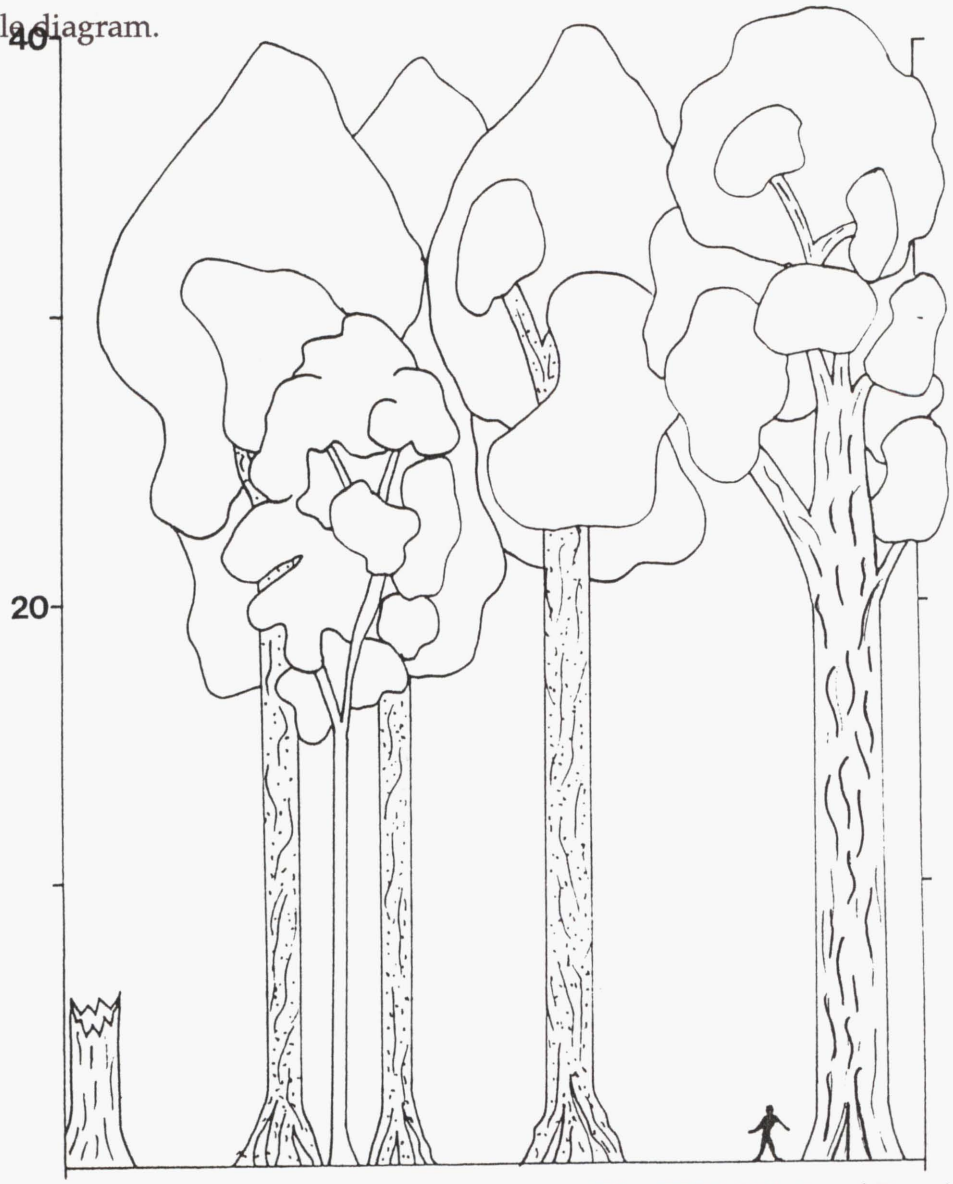
B. Profile diagram.

Figure 6.19 Dennistoun Bush Huge stand description.

A. Size class frequency distribution.



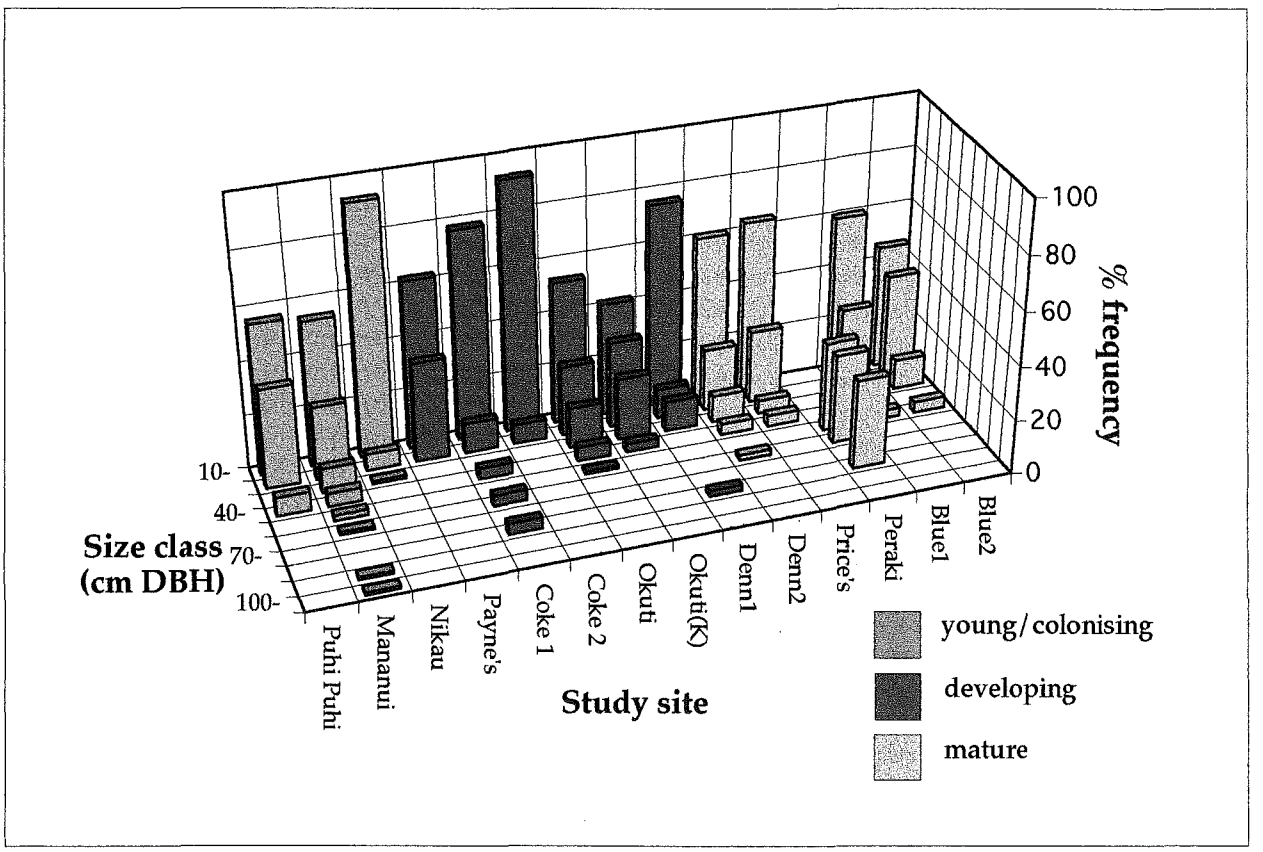
B. Profile diagram.



Angiosperms

Figure 6.20 shows the size class distribution of angiosperms at all sites. In Peraki only angiosperms over 50cm DBH were recorded. In all other sites, angiosperms are limited to the smallest size classes. Possible angiosperm perch trees from the past may now not be present and it was considered that the present small angiosperms would have little impact on the spatial structure and species composition of the current mature podocarp elememt in these forests. For this reason little angiosperm data are presented in this thesis.

Figure 6.20 Angiosperm size class frequency distribution for all sites.



The only angiosperm species to occur at all sites are mahoe and supplejack. Pigeonwood occurs at all sites except Dennistoun Bush, where the common occurrence of tree fuschia indicates frequent disturbance. The presence of titoki at Price's Valley also indicates disturbance (Hugh Wilson pers.comm.). For full species' lists and botanical names at each site see Appendix Two.

6.4 AGE CLASS DISTRIBUTIONS

6.4.1 Methods

Due to the error involved with ring counts (see section 3.4.4), 30 year age classes are used in the following age class distributions. Tree age error estimates (Table 3.5) indicate that a maximum error of 20-27 years is expected for 250 year old podocarp trees. Age classes of 30 years should therefore eliminate most of the error involved in absolute tree ageing. Age class distributions are of adults and saplings, both aged from ring counts and estimated from regressions.

6.4.2 Results

Age class distributions are of adults and saplings, both aged from ring counts and estimated from regressions, and appear in Figure 6.21. Age ranges of the podocarps (standardised from 1995) are presented in Table 6.2.

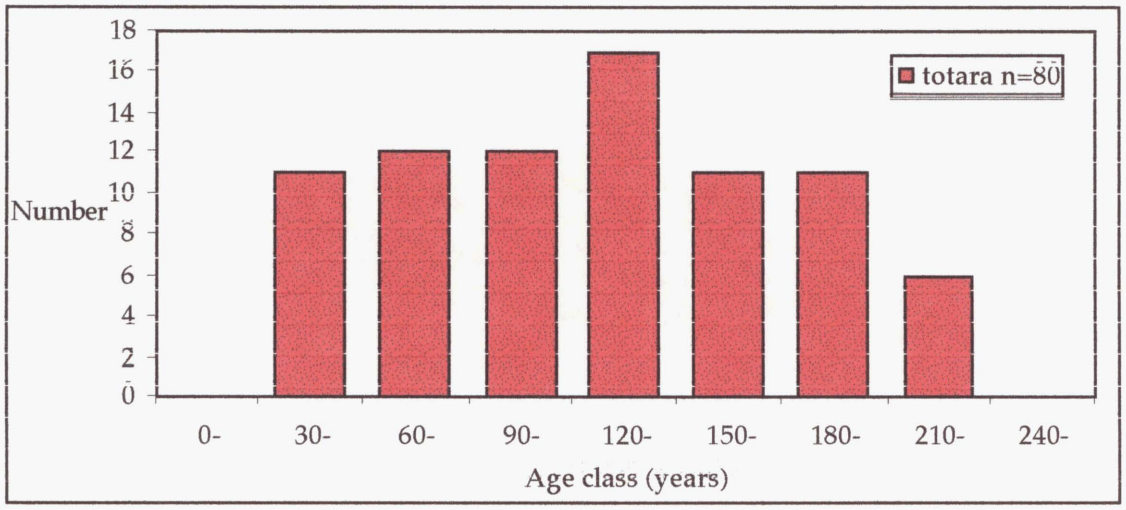
Table 6.2 Age range (years from 1995) of the podocarps in aged stands (aged from ring counts and estimated from regressions).

SITE⇓ SPECIES⇒	TOTARA	KAHIKATEA	MATAI
MANANUI	20 - 239 (219)	-	-
PUHI PUHI	103	-	95 - 148 (53)
PAYNE'S FORD	59 - 114 (55)	-	-
COKE 1	55 - 144 (89)	53 - 219 (166)	69 - 170 (101)
COKE 2	83 - 136 (53)	79	91 - 172 (81)
OKUTI VALLEY	58 - 160 (102)	-	94 - 139 (45)
OKUTI (kanuka)	61 - 159 (98)	91	116 - 142 (26)
DENN BUSH 2	36 - 216 (180)	96 - 228 (132)	102 - 140 (38)
DENN BUSH 1	145 - 268 (123)	146 - 321 (175)	240

Figure 6.21 Age class distributions for all aged stands.

PUHI PUHI S.R.

MANANUI BUSH S.R. (totara only).



PAYNE'S FORD S.R.

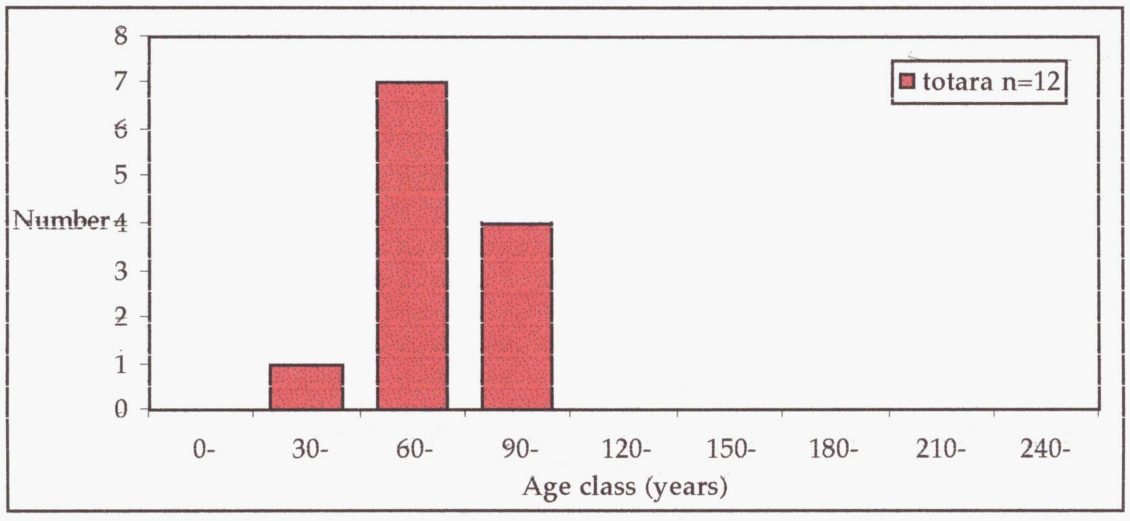


Figure 6.21 Age class distributions for all aged stands continued.

COKE COVENANT 1

COKE COVENANT 2

OKUTI VALLEY S.R.

Figure 6.21 Age class distributions for all aged stands continued.

OKUTI VALLEY S.R. kanuka

DENNISTOUN BUSH S.R. 2

DENNISTOUN BUSH S.R. 1

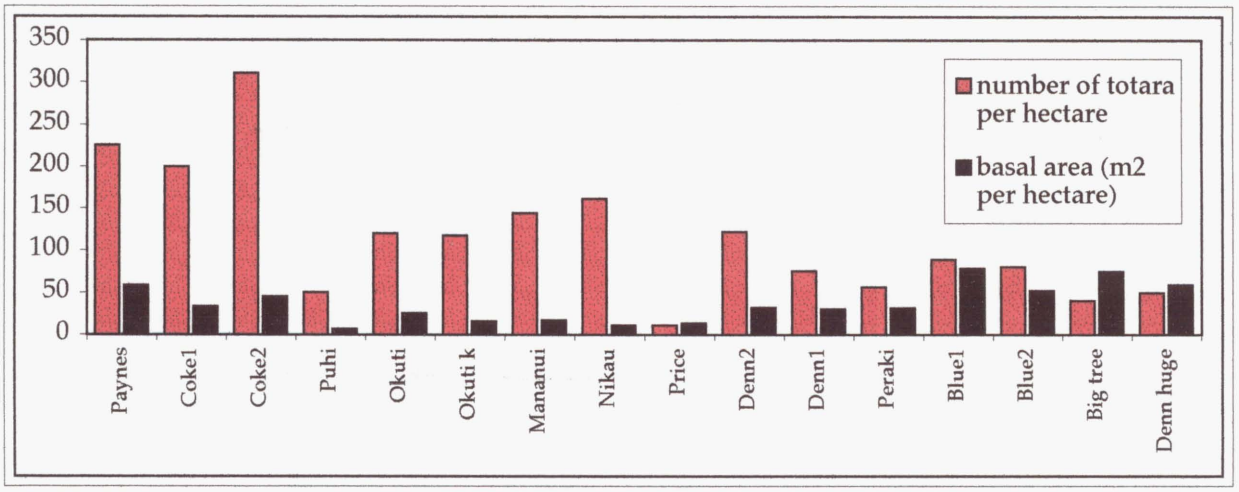
Mananui shows a normal totara age class distribution i.e. bell-shaped curve (Fig. 6.21). Puhi Puhi and Payne's Ford show slightly skewed totara and matai age class distributions, with most trees in the older age classes. Coke 1, Coke 2, Okuti, and Okuti kanuka show normal totara age class distributions but matai is more skewed to the older age classes. In Coke 1 and 2 matai enters the stand earlier than totara whereas at Okuti and Okuti kanuka matai enters the stand after totara. In all of these stands, matai ends its regeneration phase before totara.

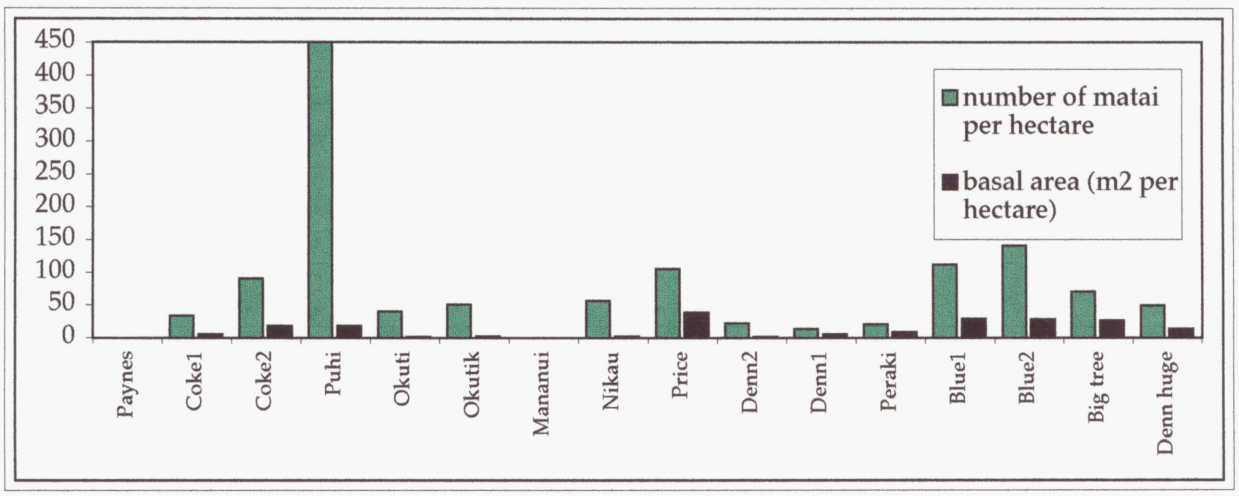
Denn I and 2 show normal totara and kahikatea age class distributions (Fig. 6.21). Matai occurs in the intermediate age classes. As with Okuti and Okuti kanuka, matai enters Denn 1 after totara and ends its regeneration phase well before totara. This may be due to dominant totara rapidly reaching the canopy and blocking light to the slower growing matai saplings, which then slowly grow to attain the canopy due to their shade tolerance ability (Ebbett & Ogden 1998).

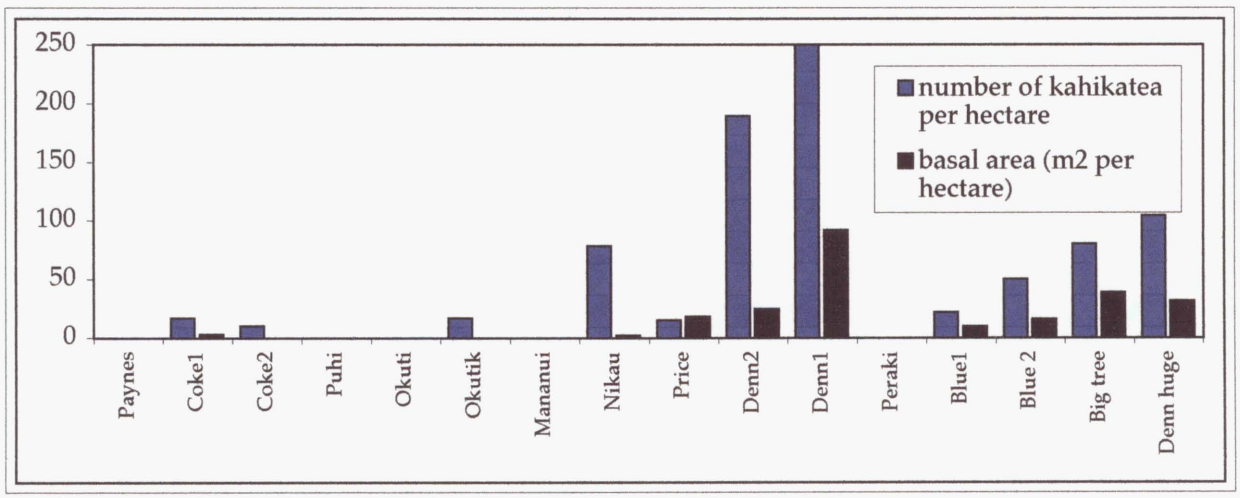
Age class distributions show that in all stands where totara and matai are present (6 of 9 aged stands), matai ends its regeneration earlier than totara. In four of these stands, matai has a more limited age range than totara. In all stands where totara and kahikatea are present (5 of 9 aged stands), kahikatea also ends its regeneration phase earlier than totara. In three of these stands, kahikatea shows the oldest individuals in the stand. Kahikatea and totara otherwise show similar age ranges (Table 6.2). Matai and kahikatea end their regeneration phase earlier than totara in over half of the stands (matai 67%, kahikatea 56%).

Figure 6.22 shows number of adult stems per hectare (≥10cm DBH) and basal area values (m^2 per hectare, saplings and adults) for all study plots. Data presented is the same as for Figure 4.6, but in this case stands are arranged from youngest (Paynes Ford) through to oldest (Denn Huge), on the basis of ring counts. Totara shows a decline in the number of adult totara trees with increasing stand age, indicating numerical dominance and perhaps self-thinning. Kahikatea shows an increase in the number of stems per hectare with increasing stand age. The trend for matai is not so clear.

Figure 6.22 Number of adult stems (≥10cm DBH) per hectare and basal area values (m^2 per hectare, saplings and adults) for all study plots.







6.5 DISCUSSION

Complementary classifications of the indigenous forests of the North Island (Nicholls 1976) and South Island (McKelvey 1984) provide the basis for the following community descriptions. Class L (softwoods) consists of four main types where lowland totara is dominant:

• Kaikawaka/totara with some silver pine and sometimes matai (McKelvey 1963). This forest type was not encountered in the present study due to its restricted distribution in North Island.

• Kahikatea/totara (Wardle 1974, 1977). Recent alluvial soils characterise the presence of totara/kahikatea/matai forest; on stonier and better drained soils kahikatea is equalled or exceeded in abundance by the other podocarps (Wardle 1974). As podsolization and gleying leads to decreased soil fertility, rimu gradually replaces kahikatea or, on better drained sites near the mountains, lowland totara. Two examples of this forest type, containing rimu and matai as well as totara/kahikatea occur in Westland; on the gravel dunes at Nikau Reserve (miro present) and the sand dunes at Mananui Bush (no miro). This forest type appears to intergrade with the following, depending upon soil type and drainage regime. An example of this intergrade was observed on the active alluvial fan at Dennistoun Bush.

• Totara/matai. This forest association is recognised by Morton, Ogden & Hughes (1984) and McSweeney (1982) to be of greatly reduced extent and one of the rarest forest types containing mature dominant lowland totara. Several examples of this forest type were encountered in the present study. Species composition ranges from almost pure matai (Puhi Puhi, Prices Valley) to totara/matai (Okuti Valley, Coke Covenant, and Peraki Saddle), to totara/matai/kahikatea (Dennistoun Bush).

• Dense mixed podocarps throughout (McKelvey 1963, 1973, Nicholls 1976, Wardle 1977). Lowland totara occurs in association with rimu, miro, matai and kahikatea. In these associations mature totara trees have a somewhat clumped distribution and regeneration is absent under the canopy or in light gaps. In the present study, dense mixed podocarps on colluvial slopes were encountered in Blue Duck Scenic Reserve. Dense mixed podocarps were also encountered at Nikau Reserve and Mananui Bush, but their position on coastal alluvium puts them in the second

classification rather than the current one, which is generally descriptive of colluvial slopes or North Island situations.

Forest types described in the present study generally agree with the classification of Nicholls (1976) and McKelvey (1984) except for the gradation seen between the totara/matai and totara/kahikatea classes. Almost pure matai forest, such as that encountered at Puhi Puhi and Prices Valley, may develop towards the totara/matai forest type given time but at present they can be considered to be a distinct forest type. Pure totara was encountered in the present study at Paynes Ford. However, one matai seedling was present and it is possible that this stand will also develop towards the totara/matai association given time.

The vertical structure of the study plots is shown in profile diagrams. Young/colonising stands generally have a continuous low podocarp canopy and seedlings are common. Developing stands generally have a continuous high podocarp canopy with a well developed angiosperm understory. Emergent totara may occur and seedlings are common. The vertical structure of mature stands are similar to that of developing stands, although the canopy is higher, more emergent totara occur, and seedlings are rare. The only senescent stand in the present study, Dennistoun Huge, has a simple vertical structure. The canopy consists of continuous emergent podocarps and the angiosperm understory is absent.

All of the aged stands show normal totara age class distributions i.e. bell-shaped curves. Age class distributions show that in all stands where totara and matai are present (6 of 9 aged stands), matai ends its regeneration earlier than totara. In four of these stands, matai has a more limited age range than totara. This may be due to dominant totara rapidly reaching the canopy and blocking light to the slower growing matai saplings, which then slowly grow to attain the canopy due to their shade tolerance ability (Ebbett & Ogden 1998). Matai may have a more specific light requirement than totara or kahikatea and so can only regenerate in these stands when light is optimal i.e. after totara saplings have established.

In all stands where totara and kahikatea are present (5 of 9 aged stands), kahikatea also ends its regeneration phase earlier than totara. In three of these stands, kahikatea shows the oldest individuals in the stand. Kahikatea and totara otherwise show similar age ranges (Table 6.2). The similar high light requirement of seedlings of these species is discussed in Ebbett & Ogden (1998). Matai and kahikatea end their regeneration phase earlier than totara in over half of the stands (matai 67%, kahikatea 56%).

Totara shows a decline in the number of adult totara trees with increasing stand age, indicating numerical dominance and perhaps self-thinning. Kahikatea shows an increase in the number of stems per hectare with increasing stand age. The trend for matai is not so clear.

The distribution and niche of lowland totara dominated forest has been described (Chapter Four), indicating the importance of soil type and landform position. Chapter Five outlines the importance of disturbance in the regeneration of lowland totara dominated forest, and the effect of landform position on disturbance regime. The results of this chapter indicate that lowland totara dominated forest develops along a defineable pathway. Stand associations have been classified into forest types, which can depend upon soil type and landform position. Forest vertical structure and age class distributions show similar patterns.

More detailed analyses of lowland totara dominated forest are presented in the following chapters. Seedling ecology is investigated (Chapter Seven), stand spatial structure is described (Chapter Eight), and stand growth through time (Chapter Nine) investigates the pattern of stand development further.

Plate11 Fast-growing kahikatea in matai-dominated Price's Valley Covenant, Banks Peninsula.

Plate 12 Adjacent *P.totara* and *P.hallii* seedlings in Nikau Scenic Reserve, Punakaiki, where hybrids between the two species occur.

Plate 13 Large lowland totara seed tree on limestone bluff in Payne's Ford Scenic Reserve, Takaka, Golden Bay.

CHAPTER SEVEN
SEEDLING ECOLOGY

7.1 INTRODUCTION AND OBJECTIVES

The objectives of this chapter are:
- To elucidate podocarp seedling ecology through an investigation of seedling position, spatial description, and light level requirements.
- To investigate the relative roles of both angiosperms and podocarps (parent trees and otherwise) in the position of seedlings.

Many factors influence the distribution and survival of seedlings. The importance of angiosperms to the distribution of podocarp seedlings has been determined from previous studies (e.g. Beveridge 1973, Norton 1991). Are seedlings preferentially distributed under angiosperms or parent trees? What factors influence the establishment and survival of podocarp seedlings?

Bird species play an important role in the dispersal of many of New Zealand's canopy dominants and perch trees can influence where seeds are dispersed to. The attractiveness of the fleshy podocarp receptacle to many forest birds makes these species well suited to bird dispersal although most seed falls directly under the parent tree (Preest 1963). Robertson & Hackwell (1995) show that native birds play an important role in the succession of kahikatea forests in South Westland, as birds are the principal agents for long distance seed dispersal of both the shrub species and kahikatea itself. In a study of podocarp regeneration following the 1886 Tarawera eruption, Burke (1974) found *P.hallii* seedlings no further than 58m from parent trees whereas *P.totara* seed had been dispersed 4.8km.

The importance of hardwood (angiosperm) tree species on bird behaviour is recognised by Preest (1963), Beveridge (1973) and McEwen (1978). Preest (1963) states that podocarp regeneration presumed to be the result of bird dispersal can be seen many kilometers from the source, frequently associated with suitable perching places. In a study of cyclic podocarp regeneration, Beveridge (1973) shows that hardwood trees develop in tree-fall gaps and grow into suitable perch trees.

Podocarp seedlings are recruited under the hardwood tree from bird dispersed seeds and grow into saplings as the hardwood tree gradually thins and dies.

In the present study, angiosperm adults were considered to be potential perch trees i.e. where birds sit after eating seeds. Parent trees are also considered 'potential' because accurate sexing was not possible at many sites due to the time of the year (i.e. parent trees were not in seed).

The location of seedlings themselves is also of interest. Are seedlings distributed randomly? Are seedlings positively or negatively associated with certain species? Spatial autocorrelation deals with the distribution of a variable such as tree size in horizontal space. Measures of spatial autocorrelation can determine if neighbouring points are more or less similar to each other with respect to some variable (such as the same species or other species) than would be expected from a random distribution of the variate values (Duncan 1992). Measures of spatial autocorrelation can be used to test for significant pattern in the spatial distribution of a variable and to describe the pattern (Legendre & Fortin 1989).

Lowland totara has long been considered a light demanding species (e.g. Cameron 1960a, McKelvey 1963) with a pioneer strategy colonising infertile or recently disturbed sites, perhaps under a nurse crop (e.g. Greenwood 1949, Beveridge 1983). There is strong evidence that lowland totara is unable to regenerate beneath a closed canopy or even in small gaps within the canopy. Its regeneration appears most vigorous in large windthrow gaps, forest margins or in open scrub and grassland (i.e. in high light or disturbed areas). If lowland totara is a light demanding species, canopy gaps would have to be very large to allow enough light to enter for totara to regenerate.

In the present study, several sites (Payne's Ford, Mananui, Nikau) show evidence of totara seedlings occurring in the open (i.e. in high light situations), rather than occurring under angiosperms. Evidence of regeneration around remnant edges was also seen at sites such as Okuti Valley (pers.obs.). Growth rate data indicates a high light requirement for the seedling growth of totara and kahikatea, whereas matai, rimu, and miro are considerably more shade tolerant (Ebbett & Ogden 1998). The present light level study was undertaken in order to further elucidate light requirements for the regeneration of the main canopy podocarps.

The following research questions are addressed in this chapter:

• Are seedlings preferentially distributed with regards to micro-topography? This is addressed by a study of seedling position.
• Do seedlings occur more frequently under podocarps or angiosperms? This is addressed by a study of seedling overhead cover.
• Are seedlings preferentially distributed closer to parent trees or potential perch trees? This is addressed by a study of seedling nearest neighbour.
• Are seedlings distributed randomly or are they grouped together (clumped distribution) or evenly-spaced (uniform distribution)? This is addressed by applying K(t) spatial analysis.
• Similarly, are two groups of seedlings distributed randomly in space with respect to each other or are they positively or negatively associated? This is addressed by applying K12(t) spatial analysis.
• What effect does litter depth have on the distribution of seedlings, and does the effect of litter depth vary under angiosperms and totara adults?
• What are the seedling-sapling-adult ratios present in the study plots and do these ratios indicate differences in regeneration strategies between the main podocarp species?
• Under what light environment do the different species occur and are there any differences between the podocarp species? This is addressed by a light level study in one of the study plots.
• Is there any evidence of a nurse crop? This is addressed in the senescent kanuka study in one of the study plots.

7.2 METHODS

Seedling ecology of the podocarps present in lowland totara dominated forest was studied through an investigation of seedling position in relation to adult perch (angiosperm) and parent trees (podocarp ≥10cm DBH). Only seedlings over 50cm high were recorded as these are considered to be established, seedlings under 50cm were considered to be ephemeral. Seedlings were defined as being over 50cm high but less than 5cm DBH, saplings were defined as being 5-9.9cm D.B.H. All seedlings and saplings present in each plot were recorded as plot locations, as outlined in section 3.3.2.

7.2.1 Seedling position

Seedling position recorded in the field as level, elevated, or depressed (position of seedling stem on the ground relative to the surrounding $4m^2$, 10 seedlings

minimum) and analysed for deviation from the assumption of random spatial distribution using X^2-tests.

7.2.2 Seedling overhead cover

Seedling overhead cover was recorded in the field as angiosperm or gymnosperm by making subjective assessments as to the overhead cover species, and analysed to test for deviations from an assumed random distribution using X^2-tests (10 seedlings minimum). Only canopy or subcanopy species were recorded as overhead cover, understorey species occurring above seedlings were excluded.

7.2.3 Distance to nearest neighbour

Distance to, and species of, nearest perch and parent adult trees (≥10cm D.B.H.) to seedlings (10 seedlings minimum) and saplings (8 saplings minimum) measured from plot maps using dividers and analysed for deviation from the assumption of random spatial distribution using X^2-tests. Less saplings occur and so sample sizes are smaller. Only individuals inside a 5 meter perimeter strip around the plot were used for this analysis due to the errors involved with calculating the nearest neighbour to individuals on the plot edge (i.e. nearest neighbours may occur just outside the plot).

7.2.4 Spatial analysis

Spatial autocorrelation of seedlings and saplings in the present study was investigated using Duncan's (1992) spatial analysis programmes. Measures of association both within (K(t)) and between species (K12(T)) were calculated using formulae outlined in Duncan (1992). Individuals in the present study were recorded as point locations with x,y co-ordinates (see 3.3.2) and so were directly imputed into the following programmes for spatial analysis.

The univariate programme for K(t) analysis calculates the function K(t) (see Ripley 1977, Diggle 1983, and Upton & Fingleton 1985) for a set of point locations in a square or rectangular plot. By running simulations the value of K(t) at any distance can be compared with that expected from a randomly distributed set of point locations. The pattern can then be described as random, clumped, or regularly dispersed at any distance up to half the length of the shortest plot side. In the present study 'neighbouring points' were defined using 2m distance classes.

The bivariate programme for K12(t) analysis calculates the function k12(t) (see Lotwick & Silverman 1982, Diggle 1983, Upton & Fingleton 1985) for two sets of point locations in a square or rectangular plot. By running simulations, the value of K12(t) at any distance can be compared with the null hypothesis of spatially independent components. Two groups of points can then be described as either independent, or positively or negatively associated with one another for any distance up to half the length of the shortest plot side. In the present study 'neighbouring points' were defined using 3m distance classes. Three metre distance classes were used in this analysis to increase sample sizes and hence any significance.

In both K(t) and K12(t) analysis, only plots with 10 seedlings minimum were used.

7.2.5 Litter depth study

The effect of litter depth on the distribution of angiosperm and podocarp seedlings was investigated through a study of litter depth in Okuti Valley Scenic Reserve. Six totara and six angiosperm adults were selected for study; all individuals had seedlings occurring beneath their canopy. For the purpose of measurement, the area under each individuals canopy was divided into north, east, south, and west sectors. Litter depth in each sector was measured to the nearest 0.5cm at 1m intervals along transects which bisected each sector. Litter depth was recorded up to four metres distance from the adult bole. The number of angiosperm and podocarp seedlings in each sector were recorded.

7.2.6 Seedling-sapling-adult ratio

Seedling-sapling-adult ratios were determined from total counts in each plot.

7.2.7 Light level study

The light environment under different overhead species was investigated through a light level study conducted in Okuti kanuka where a senescent canopy of kanuka exists under emergent podocarps. Abundant seedlings and saplings of all three canopy podocarps occur in this plot. Three replicate light sensors (Licor LI190SB quantum sensors) were placed under one individual totara, kanuka, and mahoe adult. Individuals were chosen so as to be the only species above ground level and hence measurements of incident radiation give light reaching the ground below each individual.

Incident radiation (μ Einsteins m^{-2} sec^{-1}) was measured every 5 seconds and averaged every hour from 8am to 6pm for six days from 4-10th October 1996 (see Plate 14). Data were stored in a data logger (Campbell CR10) and downloaded to a Toshiba laptop computer for analysis using single factor ANOVA on Microsoft® EXCEL5.0. Difference in total daily incident radiation (total of 11 hours mean hourly radiation from 8am to 6pm) between species was analysed for the six days with the null hypothesis of no difference in light levels between individuals.

7.2.8 Senescent kanuka study

To determine whether the now senescing kanuka was acting as a nurse crop to the podocarp species in the Okuti Valley kanuka study site, absolute kanuka ages were determined. Annual rings on six senescent kanuka trunk cross sections from in and around the study plot were examined and rings counted along three radii. Mean age was then calculated from the three radii counts. Ages of the remaining kanuka individuals in the plot were then estimated from the regression equation of the aged trees. Absolute age was then determined by adding calculated age plus a conservative figure of five years to reach 1.2m high (where diameters were measured). Size versus age of the six kanuka cross sections and regression equation appear in Appendix Three; the regression value and equation was calculated using Microsoft® EXCEL5.0.

Ages of the senescent kanuka were then compared with ages of the podocarps at the site to determine which species entered the stand first and whether or not the kanuka had acted as a nurse crop to the podocarps.

7.3 RESULTS

7.3.1 Seedling position

Seedling position results are outlined in Table 7.1. Except for totara seedlings at Payne's Ford, seedling position for each species at each site ranges from 84-100% on level sites, 2-16% on elevated sites, and 2-4% on depressed sites. Only kahikatea and matai have seedlings occurring on depressed sites. At Payne's Ford 87% of totara seedlings occur on elevated sites.

Chi-squared analysis was conducted on seedling position to test for deviation from a random distribution. As all sites were situated on relatively flat alluvial terraces,

dune ridges, or rocky bluffs, level sites were expected to be more frequent than elevated or depressed sites. Expected values used in analysis are: level 70%, elevated 15%, depressed 15%. Results are presented in Table 7.1 and all species at all sites show a deviation from random distribution (P=0.05). More seedlings than expected are encounted on level sites, except for Payne's Ford where more seedlings than expected under the assumption of random distribution are found on elevated sites. This may be a function of edaphic features or the rocky topography of the site.

Table 7.1 Seedling position (level, elevated, depressed) and Chi-squared analysis results (10 seedlings minimum). Chi-squared critical (2d.f., P=0.05) =12.84. %O = percent observed, %E = percent expected.

			Level		Elevated		Depres.		X^2
SITE	SPECIES	N	%E	%O	%E	%O	%E	%O	value
Nikau	totara	259	70	84	15	16	15	0	17.87
	hallii	12	70	100	15	0	15	0	42.86
	tot x hallii	19	70	84	15	16	15	0	17.87
	kahikatea	51	70	94	15	2	15	4	27.57
	matai	53	70	83	15	15	15	2	13.68
	miro	12	70	100	15	0	15	0	42.86
Payne's Ford	totara	24	70	13	15	87	15	0	407.0
Coke 2	totara	11	70	100	15	0	15	0	42.86
Price's Valley	matai	16	70	100	15	0	15	0	42.86
Okuti kanuka	matai	43	70	100	15	0	15	0	42.86
	kahikatea	10	70	100	15	0	15	0	42.86

7.3.2 Seedling overhead cover

The assumption of a random seedling distribution with respect to podocarp and angiosperm trees was tested using chi-squared analysis. No separation of podocarp species into parent trees and other species was made as seedling nearest neighbour analysis and spatial analysis addresses this question. Only sites with a minimum of five seedlings were used in the analysis. The results are outlined in Table 7.2. 'Observed' is the percent of seedlings occurring under either angiosperms or podocarps and '% expected' is calculated from the overall basal area values for podocarps and angiosperms at each site.

All sites and species show a deviation from the random distribution expected. Half of the results show seedlings preferentially occurring under angiosperms and half under podocarps. Perch trees and parent seed trees (or favourable microsites) both appear to influence the distribution of seedlings.

At Nikau, matai and kahikatea seedlings occur more often than expected under angiosperm trees whereas totara seedlings occur more often under podocarps. At Payne's Ford, all totara seedlings occur under angiosperms. At Price's Valley, all matai seedlings occur under podocarps.

Table 7.2 Chi-squared analysis results for seedling overhead cover. NS = not significant at P=0.05. *Number of seedlings under podocarp or angiosperm adult individuals only, seedlings occurring in the open not included.

SITE	Species	Cover	N total*	% obs.	% exp.	X^2 value	P value
Nikau	totara	podo. angio.	183	81.4 18.6	66.6 33.3	9.78	P=0.005
Payne's Ford	totara	podo. angio.	21	0 100	92.9 7.1	1308.5	P<0.001
Nikau	matai	podo. angio.	30	3.3 65.7	66.6 33.3	47.2	P<0.001
Price's Valley	matai	podo. angio.	14	100 0	85 15	17.7	P<0.001
Okuti kanuka	matai	podo. angio.	26	84 16	35 65	105.5	P<0.001
Nikau	kahik	podo. angio.	35	34.3 65.7	66.6 33.3	47.2	P<0.001

In a study on seedling and sapling distribution patterns in Mananui Bush, where overhead cover was recorded in a similar way to the present study, Norton (1991) found significantly more podocarp seedlings occurring under angiosperms than under podocarps. *Weinmannia racemosa* was the most commonly associated canopy tree with 69% of all podocarp seedlings occurring under this species (Norton 1991). Unfortunately, comparative data from the present study is not available but Norton's (1991) results also show the importance of angiosperm species in the distribution of podocarp seedlings.

7.3.3 Nearest neighbour

Nearest neighbour analysis was conducted for seedlings and saplings using the chi-squared statistic to test for differences in expected and observed frequencies of distribution between nearest neighbour species. Only sites with a minimum of ten seedlings or eight saplings were used in the analysis. The results are outlined in Table 7.3 (seedlings) and Table 7.4 (saplings). 'Observed' is the percent of seedlings and saplings being closest to either angiosperm or podocarp adult individuals (≥10cm DBH). 'Expected' is the percent of seedlings and saplings expected to be closest to either angiosperms or podocarps under the assumption of a random distribution and is calculated from number per hectare figures at each site.

Table 7.3 Chi-squared analysis results for seedling nearest neighbour. NS = not significant at P=0.05, d.f.=1. *Only seedlings > than 5m from edge. 10 minimum.

SITE	Species	N.Neigh	N total*	% obs.	% exp.	X^2 value	P value
Mananu	totara	podo. angio.	12	0 100	30 70	42.86	P<0.001
Nikau	totara	podo. angio.	87	52 48	41 59	5.00	P=0.01
Payne's Ford	totara	podo. angio.	24	45 55	53 47	2.57	NS
Coke 2	totara	podo. angio.	11	73 27	73 27	0	NS
Okuti	totara	podo. angio.	10	10 90	21 79	7.29	P=0.01
Nikau	matai	podo. angio.	31	39 61	41 59	0.165	NS
Price's Valley	matai	podo. angio.	16	0 100	24 76	31.58	P<0.001
Okuti	matai	podo. angio.	64	22 78	21 79	0.060	NS
Okuti kanuka	matai	podo. angio.	19	47 53	20 80	45.56	P<0.001
Puhi	matai	podo. angio.	39	26 74	41 59	9.30	P=0.005
Nikau	kahik	podo. angio.	27	41 59	41 59	0	NS
Denn 2	kahik	podo. angio.	16	0 100	63 37	170.27	P<0.001

Table 7.4 Chi-squared analysis results for sapling nearest neighbour. NS = not significant at P=0.05, d.f.=1. *Only includes saplings further than 5m from plot edge. 8 saplings minimum.

SITE	Species	N.Neigh	N total*	% obs.	% exp.	X^2 value	P value
Mananu	totara	podo.	8	25	30	1.19	NS
		angio.		75	70		
Nikau	totara	podo.	28	50	41	3.34	NS
		angio.		50	59		
Coke 1	totara	podo.	14	36	53	11.60	P<0.001
		angio.		64	47		
Puhi	matai	podo.	10	50	41	3.34	NS
		angio.		50	59		
Nikau	kahik	podo.	8	25	41	10.58	P=0.05
		angio.		75	59		

The small sample size at many sites (10 seedlings, 8 saplings) makes interpretation of these seedling and sapling nearest neighbour results difficult. Five of the seven seedling tests and two of the five sapling tests show podocarp youths to be closer to angiosperms than podocarp adults. When the overhead cover results are taken into account some further trends are seen. All significant kahikatea seedling and sapling results show that angiosperms play a major role in the dispersal of this species. Kahikatea seedlings preferentially occur under angiosperms and seedlings and saplings are nearest to angiosperms. Totara and matai seedlings occur under both angiosperms and gymnosperms and nearest neighbour seedling and sapling results are also variable.

Only at Price's Valley does matai occur under potential matai parent trees - an expected result as this stand is almost pure matai. However, at Okuti and Okuti kanuka (totara/matai forest) matai seedlings mainly occur under totara adults. Matai seedling nearest neighbours are also predominantly totara adults.

7.3.4 Spatial analysis

Spatial distribution of seedlings was investigated using Duncan's (1992) spatial analysis programmes, as described in section 3.2.4. Measures of association both within (K(t)) and between species (K12(t)) were calculated using formula outlined in Duncan (1992). Results are presented in Table 7.5 (K(t) analysis) and Table 7.6 (K12(t) analysis). Confidence limits in both analyses are 95%. Minimum number of

data points in K(t) analysis is ten, and K12(t) five. Due to the small sample sizes in some plots, results must be interpreted with care because the assumption of normality may be invalid for small groups when using this type of analysis (Upton & Fingleton 1985).

Only seedling to adult association analysis is presented as the only significant result in seedling to seedling association analysis was the attraction of totara and matai seedlings at 3 - 6 meters. Seedling associations with kahikatea adults are not presented as there were no significant associations. Sapling sample sizes were generally small and so saplings were not analysed with this method.

Nearly all podocarp species at all sites show a clumped distribution. Association analysis shows that all three species show an attraction to angiosperms at distances of around 3-9 metres. In Nikau Reserve, totara and matai show a repulsion from each other. Figure 7.1 shows a distinct clump of totara seedlings under a mahoe individual in Price's Valley Covenant.

Figure 7.1 Clump of totara seedlings under a mahoe individual, Price's Valley Covenant, Banks Peninsula. Data from plot map.

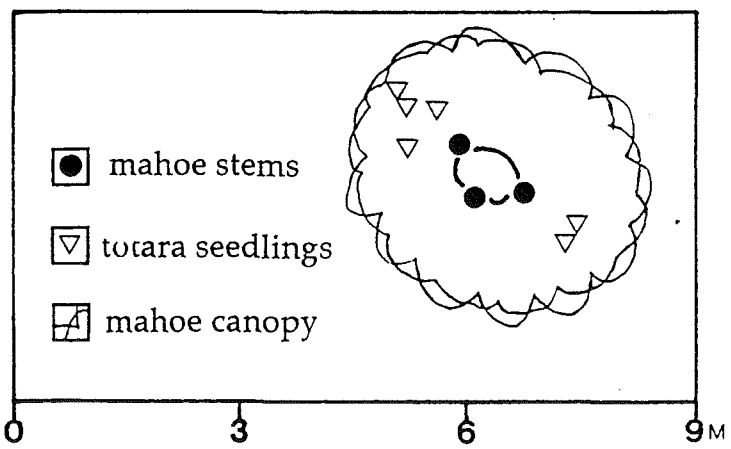


Table 7.5 K(t) seedling spatial analysis results. C= clumped, - = random, U = uniform. Two metre steps, 95% confidence limits, 10 seedlings minimum.

SPECIES ⇒	TOTARA		MATAI		KAHIKATEA	
SITE ⇓	N	2 4 6 8 10	N	2 4 6 8 10	N	2 4 6 8 10
Mananui	27	C C C C C				
Nikau	291	C C C C C	54	- - C C C	35	C C C C C
Payne's Ford	24	C C				
Coke 2	11	C C C C C				
Okuti Valley	20	C - - - -	107	C C C C C	12	C C C C -
Okuti kan.			43	C C C - -	10	- - - - -
Denn Bush 2					20	C C C C C
Price Valley			16	C C C C C		

Table 7.6 K12(t) seedling to adult spatial analysis results. A = attraction, - = independent, R = repulsion. Three metre steps, 95% confidence limits, five points minimum.

Adults⇒	ANGIOSPERM			TOTARA			MATAI		
SITE Seedlings⇒	tot	mat	kah	tot	mat	kah	tot	mat	kah
Mananui	A3								
Nikau	-	A3	A6	R3	R3	-	R3	-	-
Payne's Ford	-			-					
Coke Covenant 1	-		-	A3		-			
Coke Covenant 2	-			-			-		
Okuti Valley	-	A6	-	-	A6	-	-	-	-
Okuti kanuka	-	-	-	A3	-	-			
Denn Bush 2			-			R6			
Price's Valley	-	A9							

7.3.5 Litter depth study

Mean litter depth shows no difference between under totara adults (mean=2.97 ± 1.61 s.d., n=6) and angiosperm adults (mean=2.70 ± 1.61 s.d., n=6). Table 7.7 shows number of podocarp and angiosperm seedlings under totara and angiosperm adults. More angiosperm seedlings occur under totara adults than under angiosperm adults.

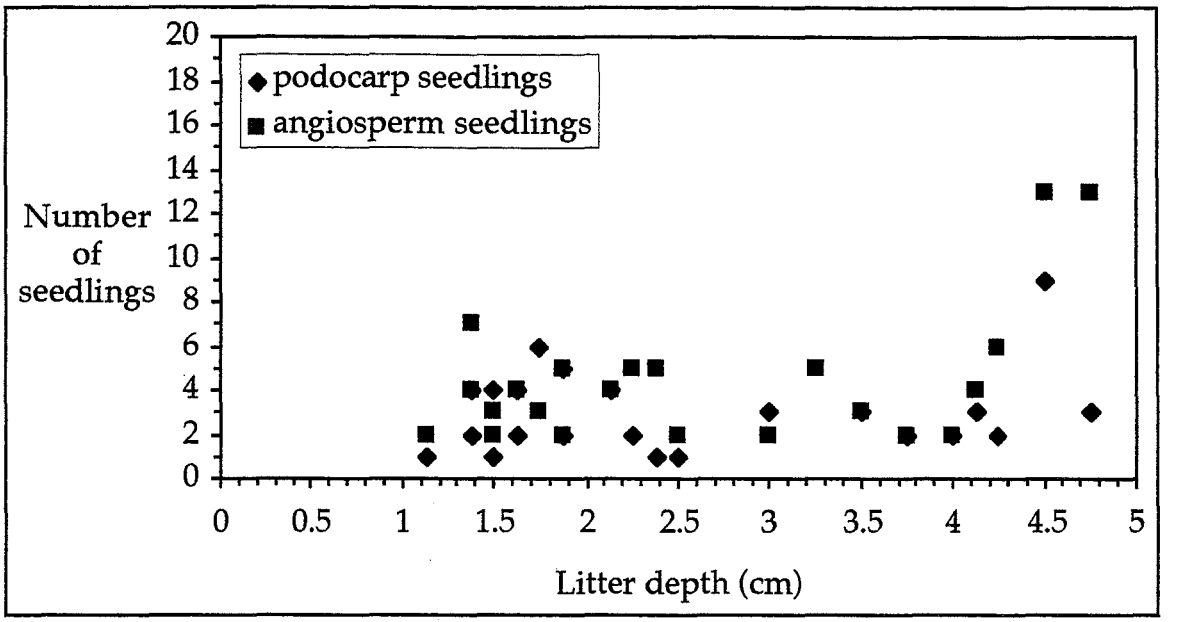
Table 7.7 Number of podocarp and angiosperm seedlings under totara and angiosperm adults.

UNDER TOTARA ADULTS n=6		UNDER ANGIOSPERM ADULTS n=6	
podocarp	angiosperm	podocarp	angiosperm
52	135	57	83

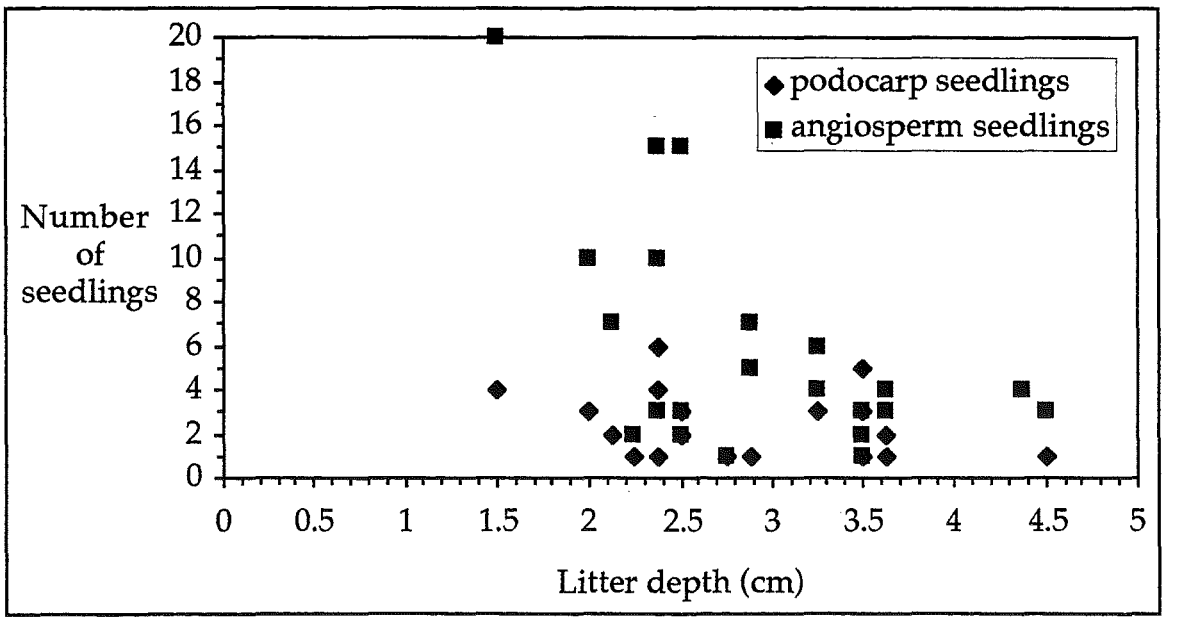
Mean litter depth in each sector was calculated and plotted against number of seedlings present in each sector. Figure 7.2A shows the number of seedlings present under angiosperm adults. No trends are seen. Figure 7.2B shows the number of seedlings present under totara adults. Podocarp seedlings show no trend. This indicates that litter depth has no effect on podocarp seedling distribution. Any effects of litter on seedling distribution may well be a function of drainage, pH, or nutrient level modification. Angiosperm seedlings appear to decrease in abundance with increasing litter depth under totara adults (Fig.7.2.B).

Figure 7.2 Number of angiosperm and podocarp seedlings versus litter depth (cm). Six angiosperm adults, six totara adults, four sectors per adult.

A. UNDER ANGIOSPERM ADULTS.



B. UNDER TOTARA ADULTS.

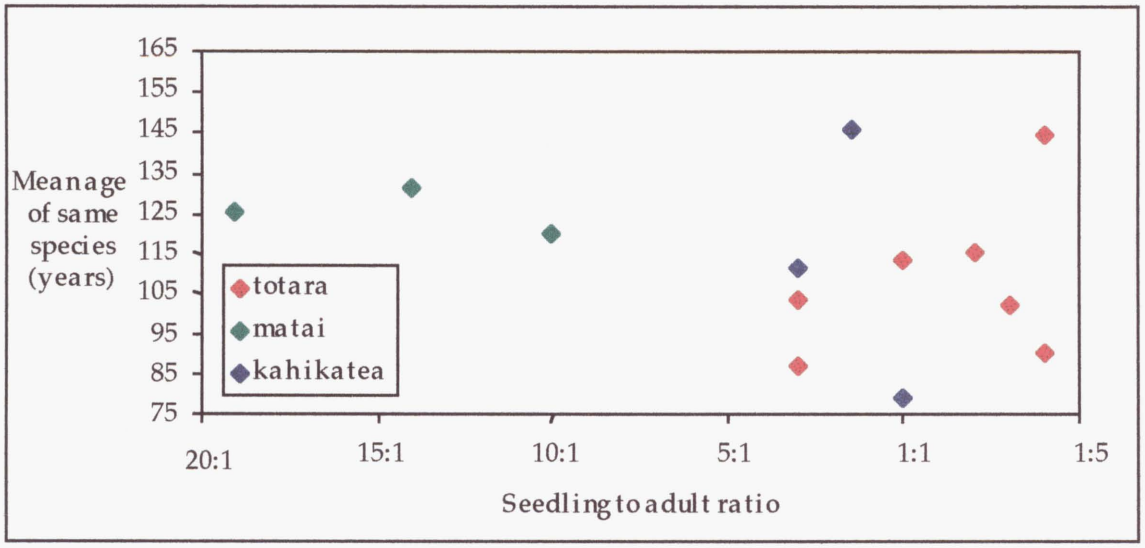


7.3.6 Seedling-sapling-adult ratios

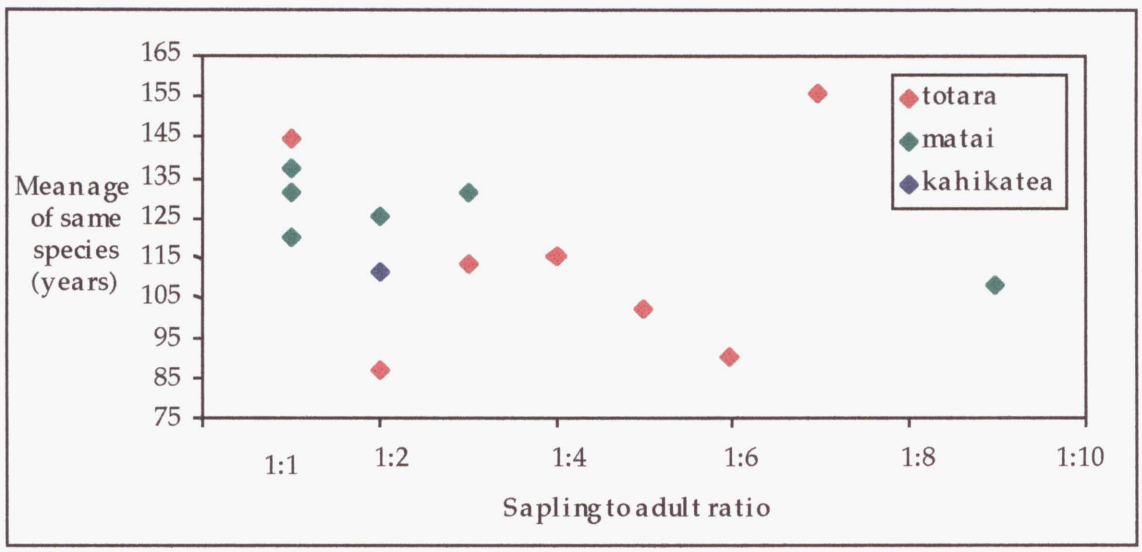
Figure 7.3 shows seedling (A) and sapling (B) to adult ratios versus mean stand age for all aged sites. Mean stand age was derived from cored individuals only. Correlation coefficients were calculated using Microsoft® EXCEL5.0.

Figure 7.3 Seedling/sapling/adult ratios for aged stands only.

A. SEEDLINGS



B. SAPLINGS



Totara shows a weak positive correlation (r=0.42) between number of seedlings and stand age whereas matai and kahikatea show weak negative correlations (matai r=-0.39, kahikatea r=-0.48). For saplings, totara again shows a positive correlation

between number of saplings and mean stand age (r=0.73) whereas matai shows a negative correlation (r=-0.78). Kahikatea is only represented by one sapling data point and so correlation coefficient analysis was not performed. Totara seedlings and saplings decrease with increasing stand age whereas matai maintains a larger population of seedlings and saplings, possibly to remain opportunistic.

7.3.7 Light level study

ANOVA results, mean hourly incident radiation per day (μ Einsteins m^{-2} sec^{-1}), and comparison of mean total daily incident radiation (total of 11 hours mean incident radiation) with Ebbett's (1992) data are outlined in Table 7.8. A significant difference in incident radiation under each species is seen (P=0.0002). Kanuka shows the highest mean light level, with totara second, and mahoe the least. Differences in incident radiation provides most of the variation, with less variation within species.

Light levels in this, and Ebbett's (1992), study were recorded over several days in summer (see Plate 14) and so are somewhat comparable although methods of measurement vary (Table 7.8C). Unfortunately, full sunlight was not measured in the present study and so comparisons of percent full sunlight cannot be made with Ebbett's (1992) data.

Light levels in the present study are all high compared to those found in the forest environment by Ebbett (1992). The results indicate that the open growth form of kanuka allows high light levels to reach the ground, providing favourable light levels for seedling growth. Totara has higher light levels underneath its crown than mahoe and in many sites seedlings occur under potential parent trees. In the present study mahoe shows the lowest light levels beneath its crown but levels are still relatively high when compared to those found by Ebbett (1992).

Table 7.8 Light level study ANOVA results, mean hourly incident radiation per day (μ Einsteins m^{-2} sec^{-1}), and comparison of total daily incident radiation (mean hourly μ Einsteins m^{-2} sc^{-1} for 11 hours) with Ebbett's (1992) data.

A. ANOVA table for total daily μ Einsteins m^{-2} sec^{-1} (total of mean hourly incident radiation for 11 hours from 8am to 6pm). Single factor, P=0.05, F critical = 3.68.

Source of Variation	d.f.	Mean squares	F observed	P value
between species	2	95246.2	15.41	0.0002
within species	15	6178.4		

B. Mean hourly incident radiation per day (μ Einsteins m^{-2} sec^{-1}).

DAY	TOTARA	KANUKA	MAHOE
1	9.65	14.05	4.53
2	6.99	14.63	4.15
3	8.56	10.64	6.13
4	6.59	11.86	4.86
5	3.12	7.13	3.01
6	8.58	15.73	6.51

C. Comparison of total daily incident radiation (mean hourly μ Einsteins m^{-2} sec^{-1} for 11 hours) under different canopy types. Present study and Ebbett's (1992) data.

PRESENT	Totara		Kanuka		Mahoe
mean daily rad.	239.2 ± 76.4		407.2 ± 104.4		160.6 ± 42.6
radiation range	103.0 - 318.6		235.2 - 519.1		99.4 - 214.8
EBBETT (1992)	Gap	Kamahi	Old totara	Pole stand	Dense
radiation range	100.4-235.9	74.4-122.8	29.5-48.2	25.1-27.9	19.3-25.1
% of full sun	30%	20%	7%	6%	5%

7.3.8 Senescent kanuka study

Table 7.9 outlines absolute kanuka and podocarp ages. Determination of podocarp absolute ages is discussed in section 3.4. Mean ages of totara, kahikatea, and kanuka are similar (84 - 95 years old). Totara and matai have individuals up to approximately 150 years old whereas kanuka only reaches 106 years old. It is possible that older kanuka was present 150 years ago but have since fallen and decayed. Matai shows the smallest age range and mean age (127 years) is greater

than the other species. If kanuka was not present 150 years ago, then results indicate that kanuka and the podocarps grew up together, rather than kanuka predating the podocarps.

Table 7.9 Absolute kanuka and podocarp ages in Okuti Valley (kanuka).

SPECIES	Number in plot	Mean age ± s.d.	Age range (years)
KANUKA	25	84 ± 15	44 - 106
TOTARA	12	95 ± 28	61 - 159
MATAI	9	127 ± 9	116 - 142
KAHIKATEA	1	91	91

7.4 DISCUSSION

• Are seedlings preferentially distributed with regards to micro-topography? All sites, except Payne's Ford, show podocarp seedlings to occur more frequently on level sites than would be expected under a random distribution. The topography of Payne's Ford is a rocky spur and so most seedlings occur on elevated sites.

• Do seedlings occur more frequently under podocarps or angiosperms? Results of seedling overhead cover analysis are all significant but variable. Half of the podocarp seedlings occur under angiosperms and half under podocarps.

• Are seedlings preferentially distributed closer to parent trees or potential perch trees? Seedling nearest neighbour results show that kahikatea is preferentially distributed closer to angiosperms. Results for totara and matai are variable.

• Are seedlings distributed randomly or are they grouped together (clumped distribution) or evenly-spaced (uniform distribution)? Almost all species at all sites show a clumped distribution. On comparison with the previous results, seedlings may be clumped around angiosperm trees (bird perch trees) or under parents (seed trees, see Plate 13). Both parent and perch trees therefore play a role in the dispersal and survival of podocarp seedlings.

• Similarly, are two groups of seedlings distributed randomly in space with respect to each other or are they positively or negatively associated? All species show

examples of being attracted to angiosperms. Totara and matai seedlings show examples of being replused from each other.

• What effect does litter depth have on the distribution of seedlings, and does the effect of litter depth vary under angiosperms and totara adults? From the limited data collected at Okuti Valley, it appears that litter depth has no effect on the abundance of podocarep seedlings. More angiosperm seedlings occur under totara adults than under angiopserm adults. Angiosperm seedling abundance decreases with increasing litter depth under totara adults.

• What are the seedling-sapling-adult ratios present in the study plots and do these ratios indicate differences in regeneration strategies between the main podocarp species? For both seedlings and saplings, totara decreases numbers with increasing stand age whereas matai maintains a large population of seedlings and saplings, possibly to remain opportunistic. Totara is a light demanding species whereas matai is shade tolerant and so can maintain seedling and sapling populations under a closed canopy.

• Under what light environment do the different species occur and are there any differences between the podocarp species? The results of the light level study indicate that the open growth form of kanuka allows high light levels to reach the ground, providing favourable light levels for podocarp seedling growth. Totara has higher light levels beneath its canopy than mahoe and in many sites seedlings occur under potential parent trees. In the present study mahoe shows the lowest light levels beneath its crown but levels are still relatively high. Light levels in the present study are all high compared to those found in the forest environment by Ebbett (1992).

• Is there any evidence of a nurse crop? Nurse crops may be an important part in the regeneration of totara dominated lowland forest by providing appropriate light levels for seedling growth. The present study indicates that nurse crops may grow up simultaneously with the podocarps, providing an improved microclimate i.e. wind shelter, moisture retention, and elevated light levels while protecting the podocarps from full sunlight.

Results of seedling ecology studies indicates that the three main canopy podocarps (totara, matai, kahikatea) have different strategies. The requirement of high light levels for the regeneration of lowland totara dominated forest has been determined. Elevated light levels generally indicate disturbance of some degree i.e. canopy

damage (see section 5.3.2). Totara and kahikatea regenerate first following medium to catastrophic disturbance which elevates light levels, followed by matai which has the most limited regeneration phase (see section 6.4.2). All species rely on bird dispersal for transport to suitable microsites. Totara can also establish under parent seed trees. The initial establishment of seedlings is affected by both perch and parent trees, and light levels.

Angiosperms play an important role in the distribution of podocarp seedlings; several results show seedlings preferentially distributed under angiosperm perch trees. After distribution to favourable sites for seedling establishment, future survival is then affected by light levels, soil conditions such as fertility and drainage, and bird behaviour. Serendipity can not be excluded as a factor in seedling distribution. In the next chapter, the spatial distribution of adult podocarps is examined.

Plate 14 Light level study under different overhead cover species; (A) kanuka, (B) lowland totara. Okuti Valley Scenic Reserve, Banks Peninsula.

A

B

CHAPTER EIGHT
SPATIAL DESCRIPTION

8.1 INTRODUCTION AND OBJECTIVES

A narrow age range in a mature conifer population may imply a seral origin (Ogden 1985). On a scale of one to a few hectares, many canopy dominants in New Zealand exhibit more or less even-aged stands, e.g. rimu and other podocarps (Herbert 1980, Katz 1980a,b), *Libocedrus* (Veblen and Stewart 1982). Many of the species which exhibit even-aged stands also have seedlings which are relatively light demanding (Ogden 1985). Ogden (1985) suggests that a stand can be regarded as relatively even-aged or a cohort defined if most of the individuals in it fall into an age range of not more than ten percent of the normally attainable age.

Limited data exists on the normally attainable range of the three main podocarps (totara, matai, kahikatea) in the present study. Data from Katz (1980b), Herbert (1980) and Bellingham (1982) indicate that a maximum attainable age for matai is approximately 800 years. Limited data exists for kahikatea but a maximum attainable age of 600 years is likely (Katz 1980b). Radiocarbon dating of one large lowland totara tree at 890± 28 years (Ebbett 1992) suggests that for totara, maximum attainable age is greater than matai or kahikatea, possibly around 900 years or more.

Analysis of tree age distributions can lead to the identification of even-aged patches, the presence of which is often compelling evidence of past disturbance (Lorimer 1985). If trees establish in even-aged patches in response to a disturbance event then the spatial distribution of tree ages will be non-random; trees of similar age will occur together (Duncan 1992). A variable such as tree age which exhibits a non-random spatial structure is said to be spatially autocorrelated.

Spatial autocorrelation deals with the distribution of a variable such as tree size in horizontal space. Measures of spatial autocorrelation can determine if neighbouring points are more or less similar to each other with respect to some variable (such as size) than would be expected from a random distribution of the variate values

(Duncan 1992). Tree locations themselves are also of interest. Are trees distributed randomly or are they grouped together (clumped distribution) or evenly-spaced (uniform distribution)? Similarly, are two groups of trees distributed randomly in space with respect to each other or are they positively or negatively associated? Measures of spatial autocorrelation can be used to test for significant pattern in the spatial distribution of a variable and to describe the pattern (Legendre & Fortin 1989).

The objective of this chapter is to investigate the spatial structure of lowland totara dominated stands. Research questions used to address this objective are:

- Are adult tree distributed at random? If not, what are the patterns, processes, and associations?
- Are the stands even-aged and does this correlate with the disturbance regime?

In order to more clearly elucidate the spatial structure within totara dominated stands, several statistical analyses were applied to the data.

8.2 METHODS

8.2.1 Plot maps of tree age/size

Plot maps show point locations and ages of trees (adults and saplings) derived from plot maps recorded in the field (see section 3.3.2). Absolute age determinations are via ring counts and regression analysis (see section 3.4.3 and 3.4.5). Ages include a correction figure for time to reach coring height. Where stands were not aged, point locations are shown as tree size (cm D.B.H.). Point locations and tree age were then used in analysis of spatial autocorrelation.

Plot maps also include groupings of trees which then appear in the figures of stand growth through time in Chapter Nine (10 year mean ring width versus time). These groups are not identified patches of even-aged trees, but rather represent groups of trees which show similar growth patterns or elucidate stand growth.

8.2.2 ANOVA methods

Differences in mean spacing of adult individuals of the three main podocarps was investigated using Microsoft® EXCEL6.0 ANOVA for one-way unequal sized population means. Are the podocarp species spaced similarily? (null hypothesis) or are they speced differently? (alternative hypothesis). Mean spacing values are

calculated for all sites with a minimum of four individuals by measuring the distance between neighbouring adults of the same species off plot maps.

8.2.3 K(t) and K12(t) analysis methods (size)

Spatial distribution of adults in the present study was investigated using Duncan's (1992) spatial analysis programmes. Measures of association both within (K(t)) and between species (K12(t)) were calculated using formulae outlined in Duncan (1992) and described in section 7.2.4. Individuals in the present study were recorded as point locations with x,y co-ordinates (see 3.3.2) and so were directly imputed into the following programmes for spatial analysis.

Using K(t) analysis, the spatial pattern of adults can be described as random, clumped, or regularly dispersed at any distance up to half the length of the shortest plot side. In the present study 'neighbouring points' were defined using 2m distance classes. Using K12(t) analysis, two groups of points can then be described as either independent, or positively or negatively associated with one another for any distance up to half the length of the shortest plot side. In the present study 'neighbouring points' were defined using 3m distance classes. Three metre distance classes were used in this analysis to increase sample sizes and hence any significance.

8.2.4 Spatial autocorrelation analysis (age)

Spatial autocorrelation of tree age was investigated using Moran's I coefficient analysis programme (Duncan 1992). The programme determines whether neighbouring points are more or less similar in age than would be expected from a random distribution of tree age. Point locations were recorded in the field and tree ages determined via ring counts and regression analysis. 'Neighbouring points' were defined using three metre distance classes. The first distance class was 0 - 3m, the second >3 - 6m, and so forth up to the length of the longest plot side. For each distance class, a pair of trees were considered neighbours if they were within the distance apart for that distance class.

Moran's I coefficient (Moran 1950) was calculated as a measure of spatial autocorrelation for each distance class using Duncan's (1992) programme. The assumption of randomisation is used as a null hypothesis (Upton & Fingleton 1985). Under the null hypothesis, Moran's I coefficient (I(d)) is asymptotically normal with an expected value E[I(d)] of 0. Values I(d)>0 are positively spatially

autocorrelated and indicate that point locations tend to have a similar age. Values I(d)<0 are negatively spatially autocorrelated and indicate that point locations tend to have dissimilar ages (Duncan 1992).

Moran's I coefficient analysis was conducted for all plots with aged trees (saplings and adults). Tree ages used are those calculated directly from ring counts and those estimated from size versus age regressions (see section 3.4.5.). Distance classes that contained less than 10 pairs of neighbouring points were excluded from analysis because the assumption of normality may be invalid for small groups (Upton & Fingleton 1985).

The significance of deviations from the expectation of randomness was tested by calculating the variance of I(d) under the null hypothesis of randomisation. Standard normal deviates, Z(d), were calculated for each distance class. The 0.05 significance level is 1.96 (Duncan 1992) and indicated on each spatial correlogram by dotted lines. Variation in spatial autocorrelation was examined by plotting values of Z(d) against distance class, resulting in a correlogram which provides a description of the spatial structure (Duncan 1992). For example, positive autocorrelation in small distance classes reflects the association of trees of similar age within patches. Negative autocorrelation in larger distance classes indicates differently aged patches.

In the present study Moran's I coefficient analysis was used to identify whether plots contained all even-aged trees or patches of even-aged trees. Patches were not further investigated.

8.3 RESULTS

8.3.1 ANOVA results

ANOVA results are presented in Table 8.1. F observed (4.447) is greater than F critical (4.2421), P=0.01, and so the alternative hypothesis of different spacing between the three species can be accepted. No separation of the species is made in this analysis and so the more detailed spatial analysis programmes of Duncan (1992) were applied to individual point locations at each site.

Table 8.1 Analysis of variance for mean adult spacing for all sites with 4 points minimum. 99% confidence limits, 2-tailed test, F critical (2,27) = 4.2421.

A. Data.

	TOTARA	MATAI	KAHIKATEA
number of sites	14	10	6
mean spacing (m)	5.76	7.77	4.15
standard deviation	2.21	3.06	1.43
variance	4.90	9.36	2.05

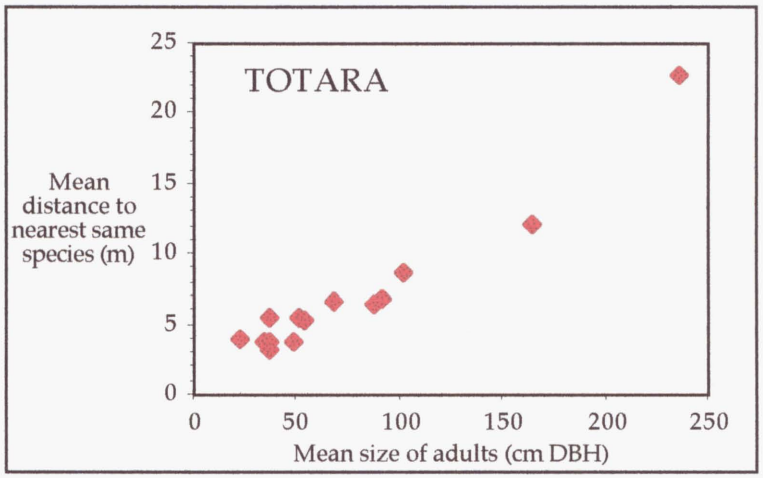
B. ANOVA table.

Source of var.	d.f.	Sum Squares	Mean Squares	F observed
among group	2	52.12	26.06	4.447
within group	27	152.12	5.86	
TOTAL	29	210.24		

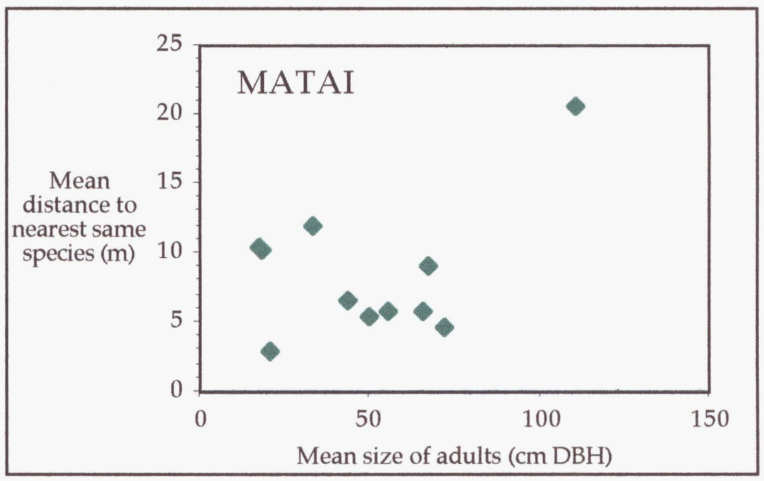
Mean adult spacing (distance to nearest same species) versus mean adult size and mean number of adult stems for the three main podocarp species are presented in Figures 8.1. and 8.2. Correlation coefficients were calculated using Microsoft® EXCEL6.0.

Figure 8.1 Mean adult spacing (distance to nearest same species) versus mean adult size (≥10cm D.B.H.).

Figure 8.1 shows mean adult size versus mean adult spacing. Totara shows the most significant positive correlation (r=0.97) indicating that this species becomes more widely spaced with increasing tree size.



Matai (r=0.42) and kahikatea (r=0.56) show weak positive correlations between size and spacing.



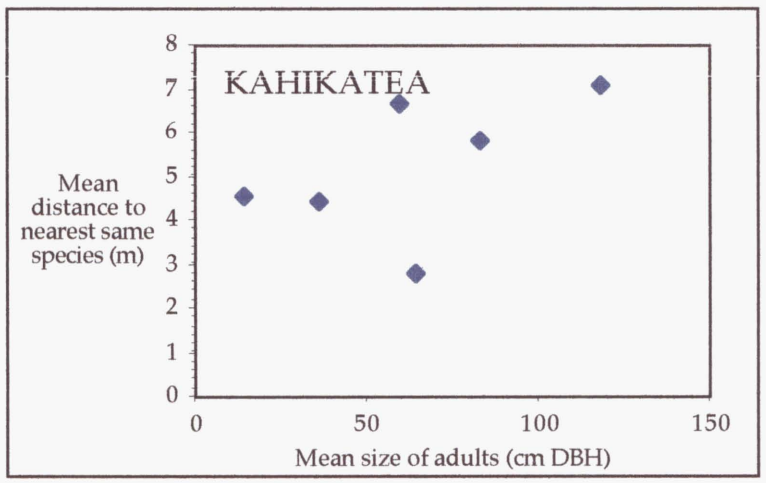
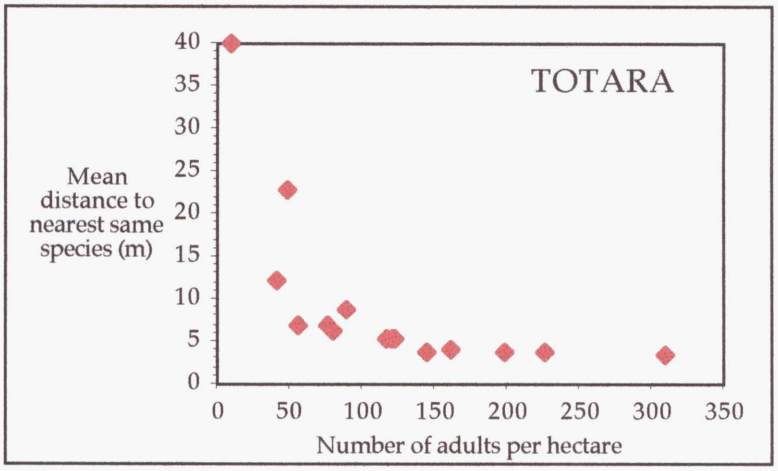
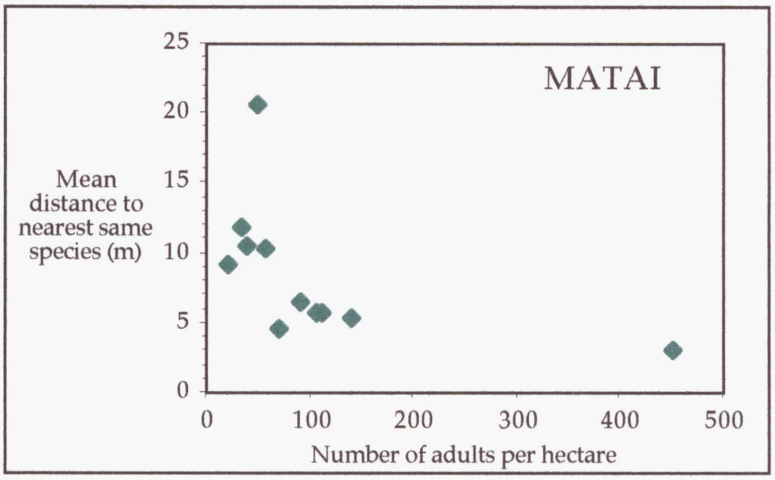


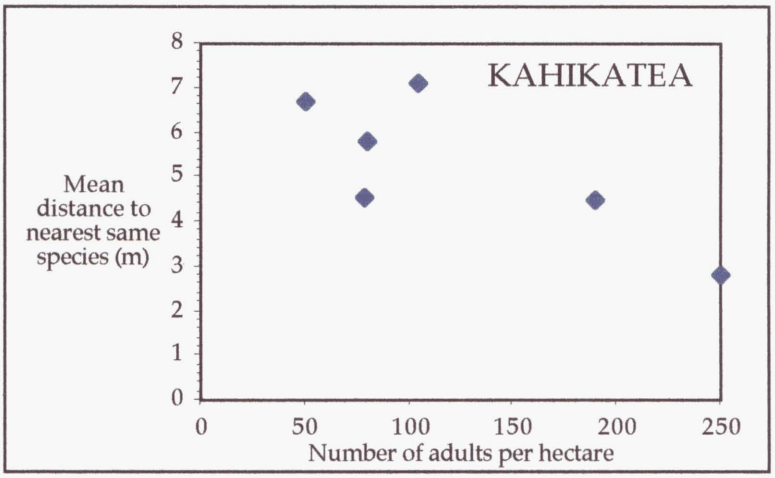
Figure 8.2 Mean adult spacing (distance to nearest same species) versus number of adult stems per hectare (≥10cm D.B.H.).

Figure 8.2 shows number of adult stems per hectare versus mean adult spacing (distance to nearest same species). All three species show negative correlations between number of adults per hectare and mean spacing (totara r=-0.60, matai r=-0.52, kahikatea r=-0.79), suggesting self-thinning.

As the mean size of podocarp adults increases, the number of adults per hectare decreases and adult spacing becomes wider.







8.3.2 K(t) and K12(t) analysis results

Results are presented in Table 8.2 (K(t) analysis) and Table 8.3 (K12(t) analysis). Minimum number of data points in both analyses is five, ninety-five percent confidence limits are generated from 19 simulations of the random point process. Due to the small sample sizes in some plots, results must be interpreted with care because the assumption of normality may be invalid for small groups (Upton & Fingleton 1985).

While sample sizes are small for many stands, some results are discernible. Totara and kahikatea show a certain degree of clumping in several stands whereas matai is randomly distributed throughout the stands except for in Blue Duck 2. The young/colonising stands of Mananui and Nikau show the most clumped podocarp distributions. Totara is clumped at all distances in Mananui, possibly reflecting the limitation of totara to certain dune positions. Kahikatea is clumped in Nikau Reserve at distances up to 6m, suggesting the limitation of this species to its preferred microsites, possibly damp depressions.

Adults of all three podocarp species show an example of repulsion from angiosperms at distances of 3 to 9 meters. In Denn Bush 1, kahikatea shows a repulsion from totara at distances of 6 meters i.e. there are less kahikatea and totara trees spaced at this distance than would be expected under the assumption of random distribution. The totara - matai relationship shows interesting results. Examples of both attraction and repulsion are present, suggesting a unique relationship between these two species.

Table 8.2 K(t) adult spatial analysis results. C= clumped, - = random, U = uniform. Two metre steps, 95% confidence limits, five points minimum.

SPECIES ⇒	TOTARA		MATAI		KAHIKATEA	
SITE ⇓	N	2 4 6 8 10	N	2 4 6 8 10	N	2 4 6 8 10
Mananui	73	C C C C				
Nikau	29	- - - - -	10	- - - - -	14	C C - - -
Payne's Ford	9	- -				
Coke 1	23	- - - - -				
Coke 2	30	- - - - -	10	- - - - -		
Okuti Valley	18	- - - - -	6	- - - - -		
Okuti kan.	12	C - - - -				
Denn Bush 2	11	- - - C -			17	- - C - -
Denn Bush 1	6	- - - - -			20	- - - - -
Price Valley			21	- - - - -		
Peraki Sad.	25	- - - - -	9	- - - - -		
Blue Duck 1	8	- - - - -	10	- - - - -		
Blue Duck 2	8	C - - - -	15	- U - - -	5	- - - - -

Table 8.3 K12(t) adult to adult spatial analysis results. A = attraction, - = independent, R = repulsion. Three metre steps, 95% confidence limits, five points minimum.

SITE ⇓	ANGIOSPERM ADULTS			TOTARA ADULTS	
ADULTS ⇒	TOTARA	MATAI	KAHIK	MATAI	KAHIK
Mananui	-				
Nikau	-	-	-	A3	-
Payne's Ford	-				
Coke 1	-				
Coke 2	-	R6		R6	
Okuti Valley	-	-		A6	
Okuti kan.	-				
Denn Bush 2	R6		R3		-
Denn Bush 1	R6-9		-		R6
Price Valley		-			
Peraki Sad.				-	
Blue Duck 1	-	-		-	
Blue Duck 2	-	-	-	-	-

8.3.3 Angiosperms

Univariate spatial analysis (K(t)) was also performed for angiosperms. Table 8.4 outlines these results. In several of the young/colonising and developing stands (Mananui, Coke 1 and 2), angiosperms show a clumped distribution in almost all distance classes. Blue Duck 1 is a mature stand and angiosperm distribution trends towards being uniform at spatial distances of 4 - 8m, possibly a reflection of the maturity of this stand.

Table 8.4 K(t) adult angiosperm spatial analysis results. C= clumped, - = random, U = uniform. Two metre steps, 95% confidence limits, five points minimum.

SITE	N	2	4	6	8	10
Mananui	203	C	C	C	C	C
Nikau	86	-	-	-	-	-
Payne's Ford	8	-	-			
Coke 1	27	-	C	C	C	C
Coke 2	14	C	C	C	C	C
Okuti Valley	89	-	-	-	-	-
Okuti kan.	42	-	-	-	-	-
Denn Bush 2	45	-	-	-	-	-
Denn Bush 1	51	-	-	-	-	-
Price Valley	79	-	C	C	-	-
Blue Duck 1	38	-	U	U	-	-
Blue Duck 2	28	-	-	-	-	-

8.3.4 Plot maps and spatial correlograms

In the following figures, plot maps of tree location (size or age) and correlograms from spatial autocorrelation analysis (age) are given. Where stands were aged, plot maps show tree age and spatial correlograms of tree age are given. Where stands were not aged, plot maps show tree size and no spatial correlograms are shown. The general colour scheme is again adopted for consistency and ease of graph interpretation: totara (red), matai (green), kahikatea (blue), miro (pale yellow), rimu (yellow).

Figures of stand spatial descriptions appear in the following order:

Young/colonising

- Puhi Puhi Scenic Reserve (Fig. 8.3).
- Mananui Bush Scenic Reserve (Fig. 8.4).
- Nikau Scenic Reserve (Fig. 8.5).

Developing stands

- Payne's Ford Scenic Reserve (Fig. 8.6).
- Coke Covenant 1 (Fig. 8.7).
- Coke Covenant 2 (Fig. 8.8).
- Okuti Valley Scenic Reserve (Fig. 8.9).
- Okuti Valley Scenic Reserve kanuka (Fig. 8.10).
- Dennistoun Bush Scenic Reserve 2 (Fig. 8.11).

Mature stands

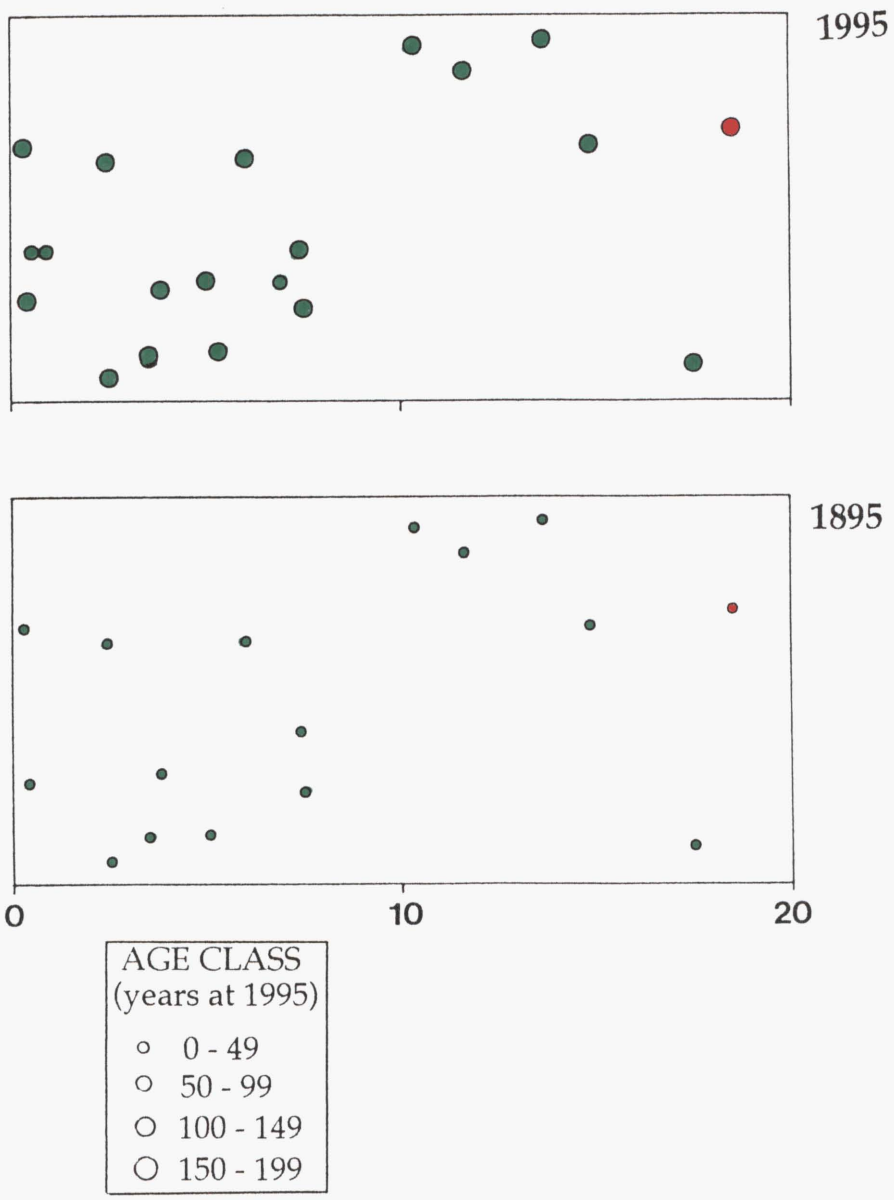
- Dennistoun Bush Scenic Reserve 1 (Fig. 8.12).
- Price's Valley Covenant (Fig. 8.13).
- Peraki Saddle Scenic Reserve (Fig. 8.14).
- Blue Duck Scenic Reserve 1 (Fig. 8.15).
- Blue Duck Scenic Reserve 2 (Fig. 8.16).
- Big Tree Peel Forest (Fig. 8.17).

Senescent stands

- Dennistoun Bush Huge (Fig. 8.18).

Figure 8.3 Puhi Puhi Scenic Reserve spatial description.

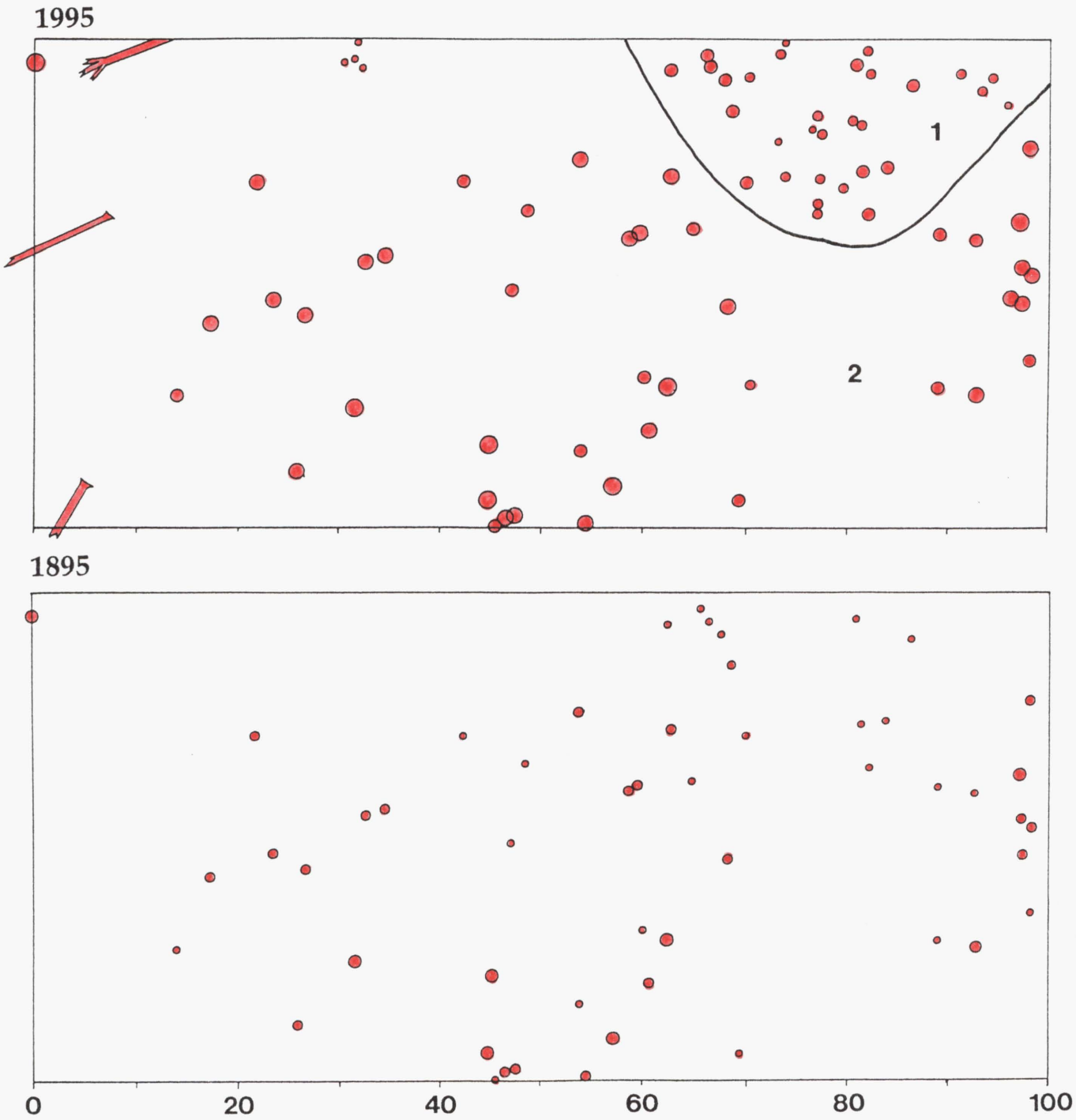
A. PLOT MAP (age).



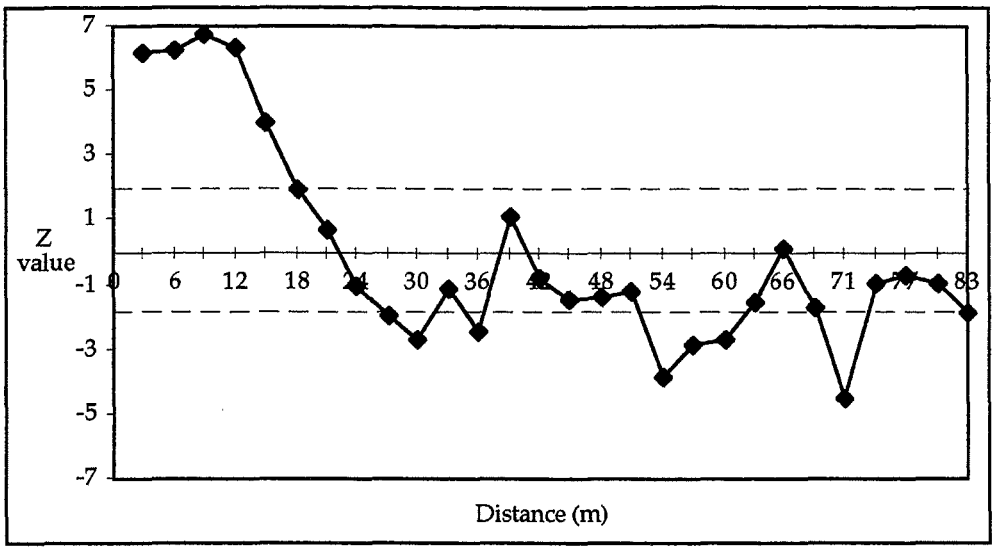
Puhi Puhi Scenic Reserve is an almost pure matai stand on an alluvial terrace. Spatial correlogram is not presented as sample size was too small. Age class frequency (see Fig. 6.21 and Table 6.2) shows a narrow age range for matai adults (53 years), suggesting that this stand is even-aged and all of the trees regenerated within the same phase, possibly as a result of river course change.

Figure 8.4 Mananui Bush Scenic Reserve spatial description.

A. PLOT MAP (age, totara only).



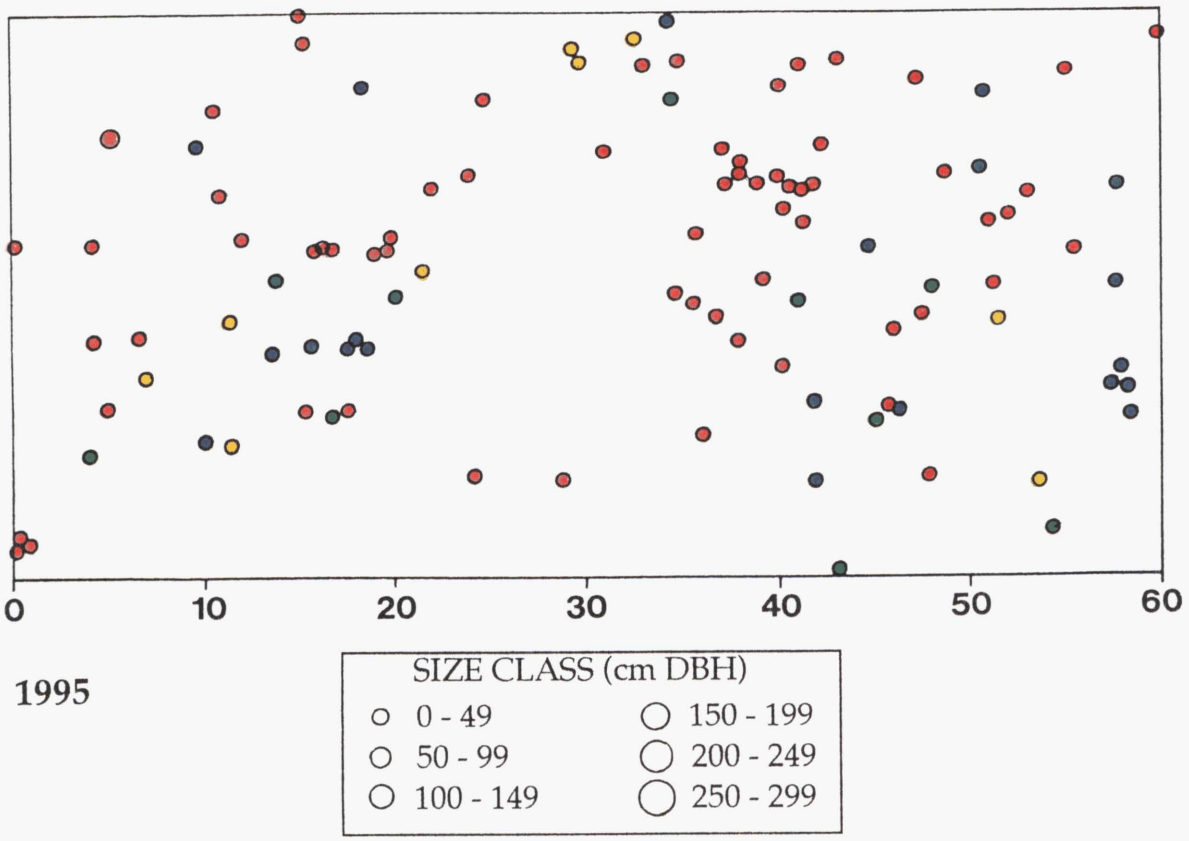
B. SPATIAL CORRELOGRAM (totara only).



Mananui Bush Scenic Reserve (Fig. 8.4) is classified as dense mixed podocarp although totara is numerically dominant. Plot map shows a distinct area of younger trees in the seaward end of the plot which are regenerating on new colonisation surfaces created by sea level fluctuations. This clump of younger trees is shown in the spatial autocorrelation diagram, where several different patches also occur (Fig. 8.4B). Adult spatial analysis (Table 8.8) also shows clumping of totara adults at all distances, perhaps indicating favourable dune positions. Age class frequency (see Fig. 6.21 and Table 6.2) shows a wide range of tree ages (239 years), reflecting the different regeneration phases as a response to sea level change and forward colonisation of the dunes.

Figure 8.5 Nikau Scenic Reserve spatial description.

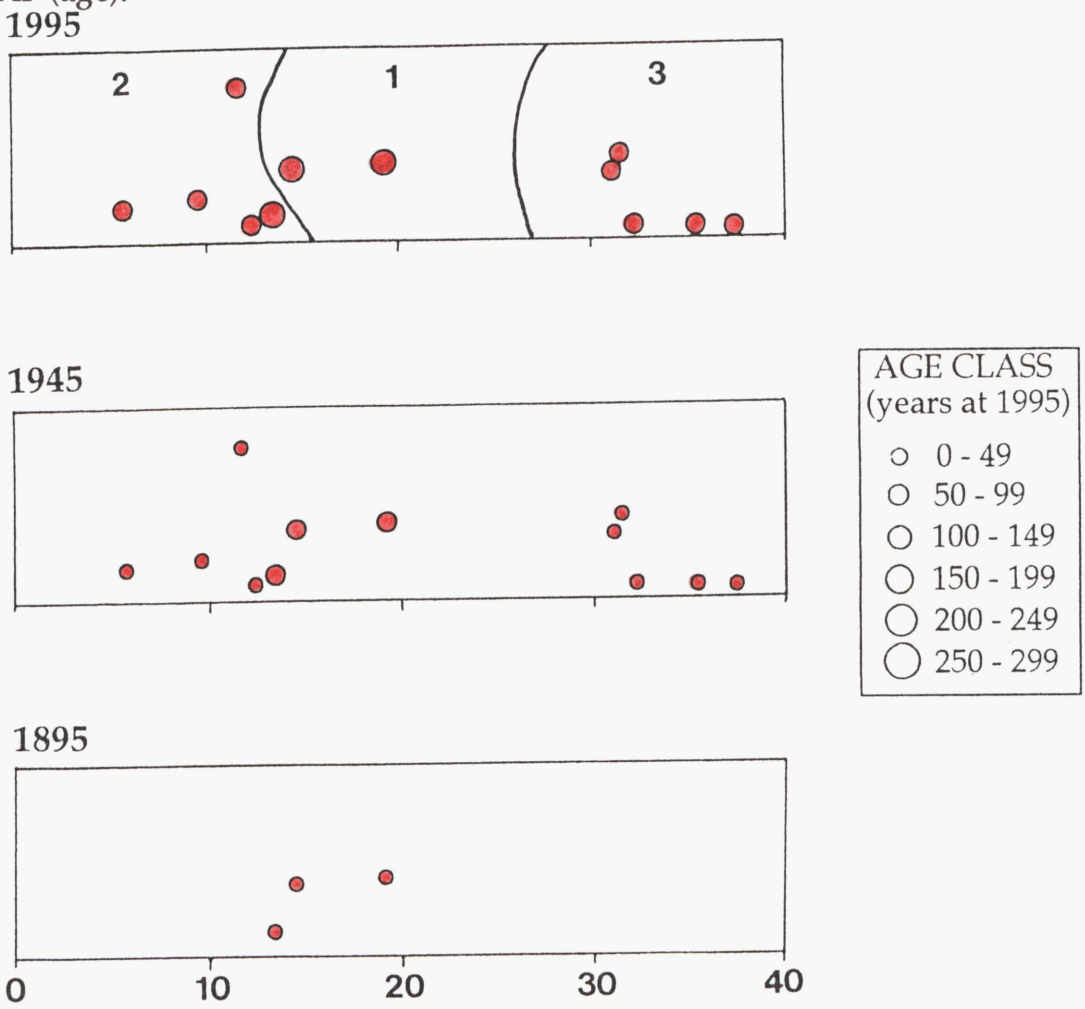
A. PLOT MAP (size).



Nikau Scenic Reserve is colonising gravel dunes (see Plate 6) and is classified as dense mixed podocarps. All individuals are small and many seedlings occur in open areas. Kahikatea adults show clumping (Table 8.2). This stand was not aged due to the wai tapu status of the reserve but size class frequency distribution (see Fig. 6.6) shows all of the podocarps to be limited to the smaller size classes, suggesting that this stand is also even-aged, regenerating in response to new colonisation surfaces.

Figure 8.6 Payne's Ford Scenic Reserve spatial description.

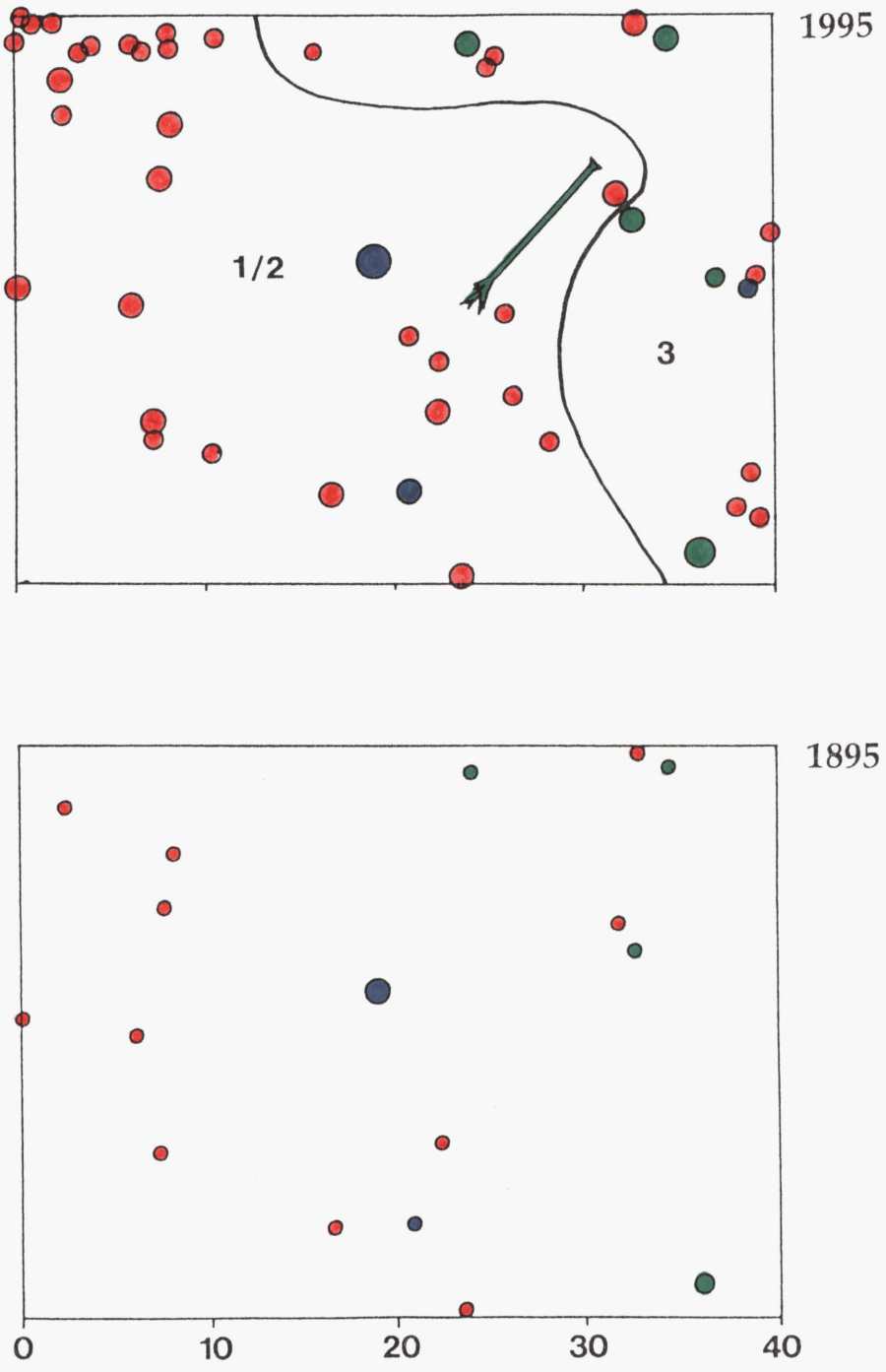
A. PLOT MAP (age).



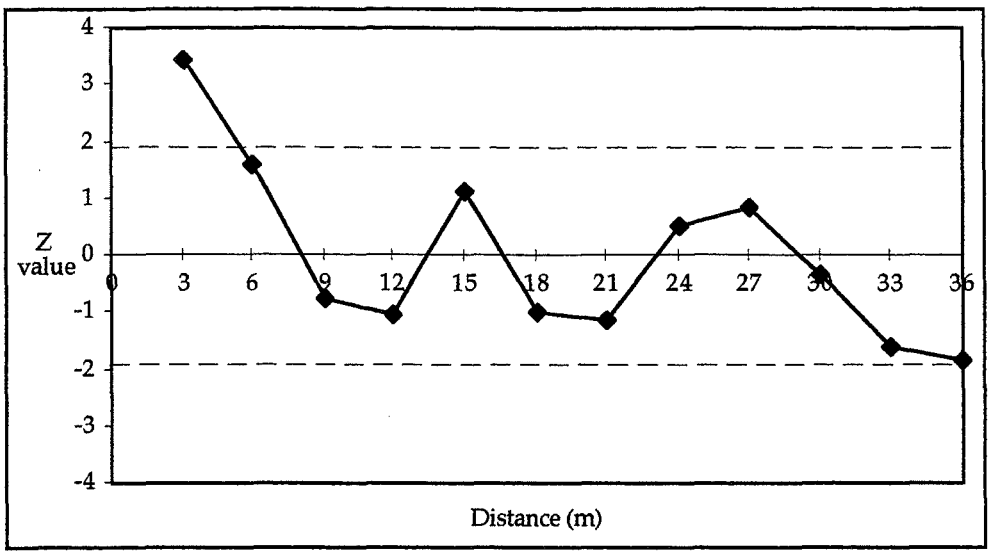
Payne's Ford Scenic Reserve occurs on a limestone bluff and is pure totara. Age class frequency (see Fig. 6.21 and Table 6.2) shows a narrow age range (55 years) and so this stand can be considered to be even-aged with all the trees regenerating in the same phase.

Figure 8.7 Coke Covenant 1 spatial description.

A. PLOT MAP (age).



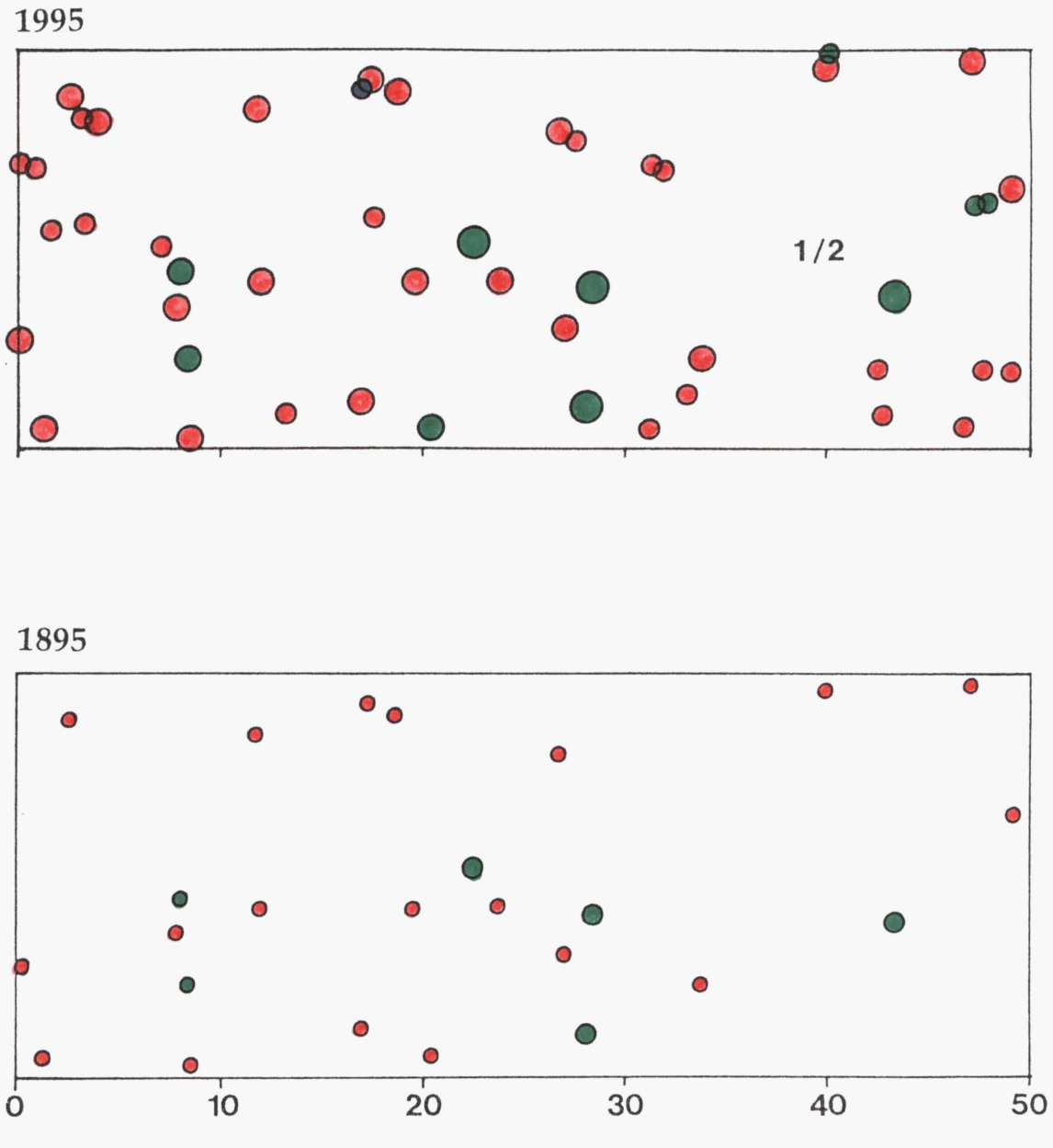
B. SPATIAL CORRELOGRAM.



Coke Covenant 1 (Fig. 8.7) and Coke Covenant 2 (Fig. 8.8) occur on the Aorere river delta within 200m of each other. These stands undergo regular flooding. Spatial correlograms and age class distributions are similar. Coke 1 shows one 6m patch of evenly-aged individuals (Fig. 8.7B) whereas all of Coke 2 is shown to be even-aged (Fig. 8.8B). Age class frequency (see Fig. 6.21 and Table 6.2) shows Coke 2 to have the most limited age range (totara = 53 years, matai = 81 years), as would be expected for an even-aged stand. Coke 1 has a wider age range (totara = 89 years, matai = 101 years), as would be expected if different patches occur.

Figure 8.8 Coke Covenant 2 spatial description.

A. PLOT MAP (age).



B. SPATIAL CORRELOGRAM.

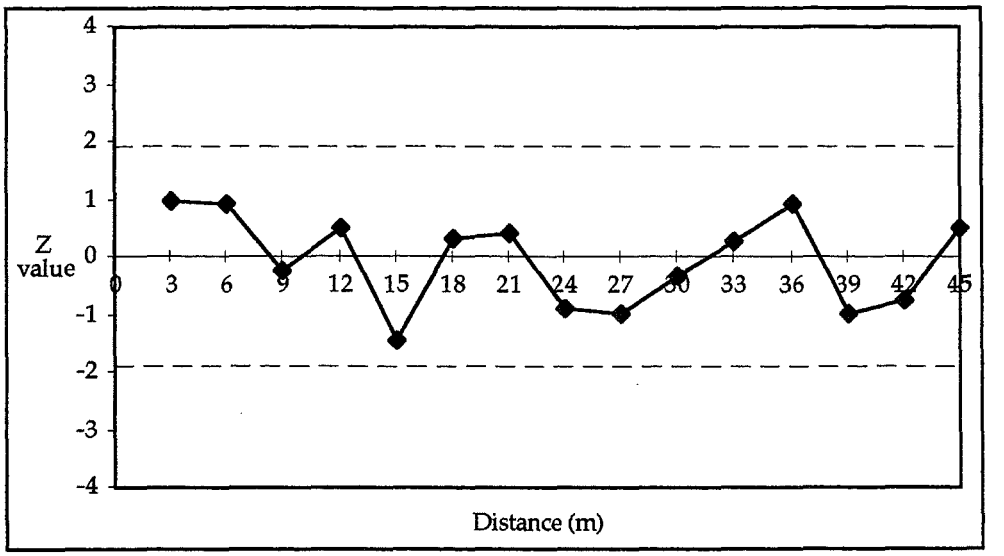
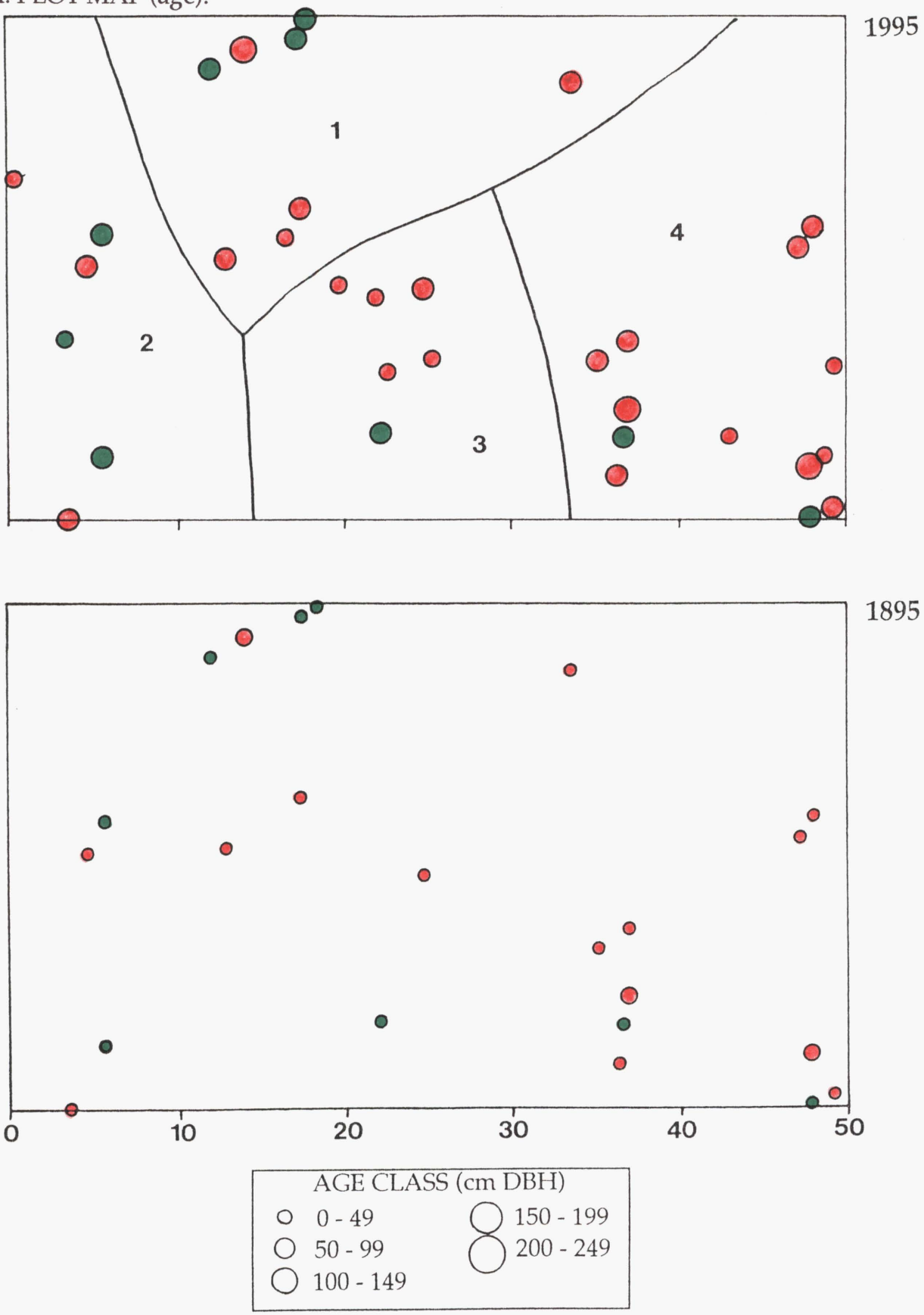
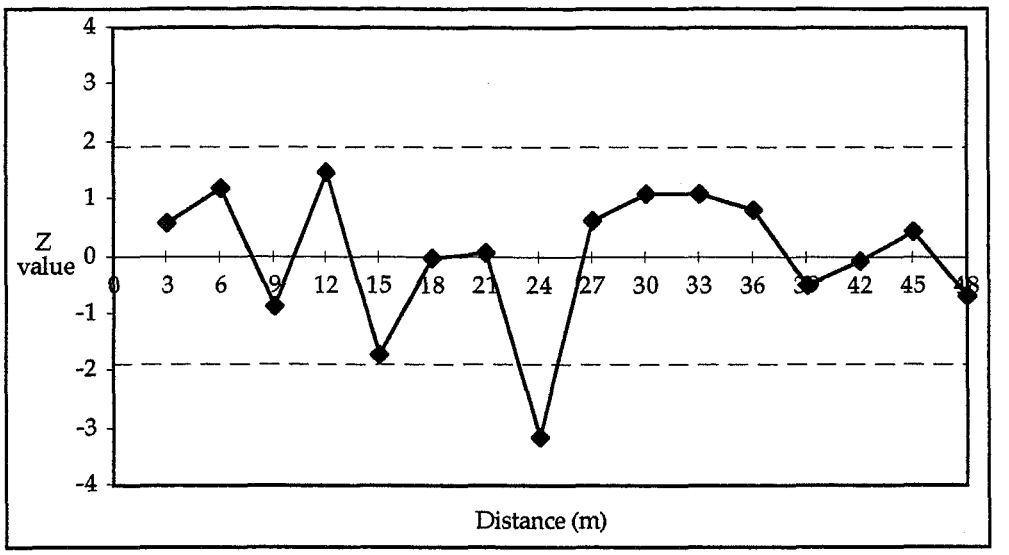


Figure 8.9 Okuti Valley Scenic Reserve spatial description.

A. PLOT MAP (age).



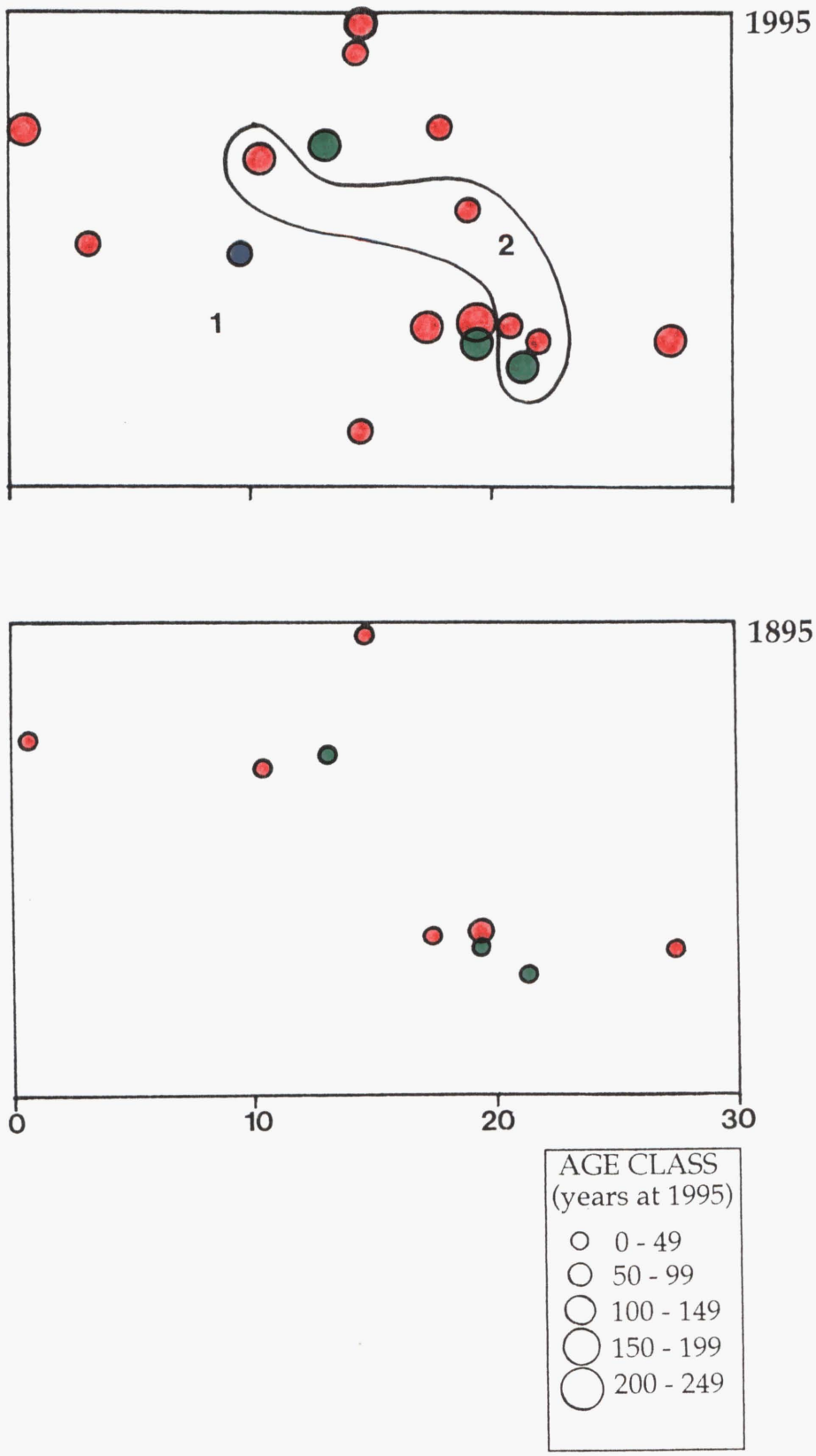
B. SPATIAL CORRELOGRAM.



Okuti Valley shows differently aged patches at distances of 24m (Fig. 8.9B) whereas Okuti kanuka shows an even-aged patch of 12m in size (Fig. 8.10B). Plot maps and resulting stand growth diagrams show a complex mosaic of groups of trees which exhibit different growth rates. Age class frequency (see Fig. 6.21 and Table 6.2) shows a wide range of ages for totara (Okuti = 102 years, Okuti kanuka = 98 years), as would be expected if differently aged patches were present. In both stands matai has a very limited age range (Okuti = 45 years, Okuti kanuka = 26 years). These stands occur on an old landslip which has been subject to fire. The disturbance regime is therefore patchy, resulting in the variable tree ages.

Figure 8.10 Okuti Valley Scenic Reserve kanuka spatial description.

A. PLOT MAP (age).



B. SPATIAL CORRELOGRAM.

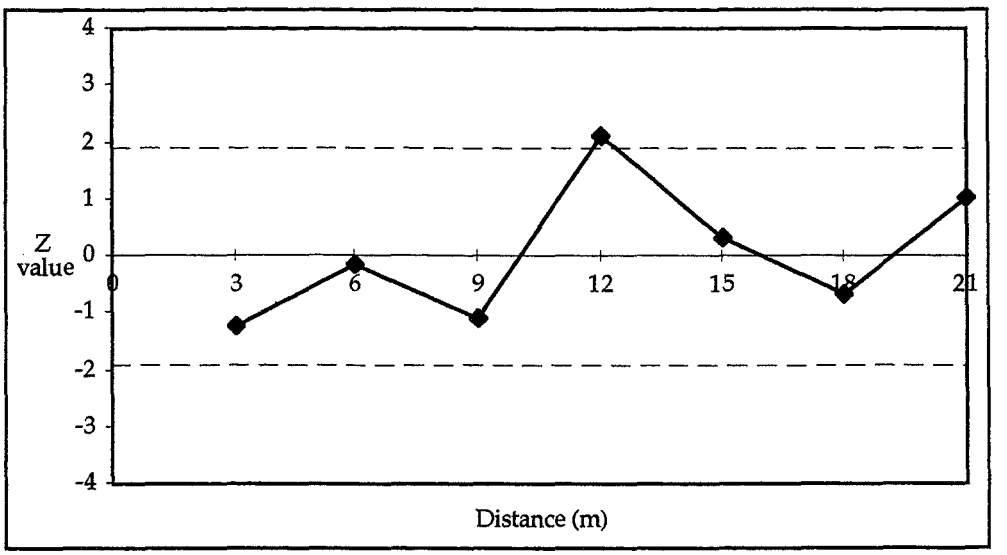
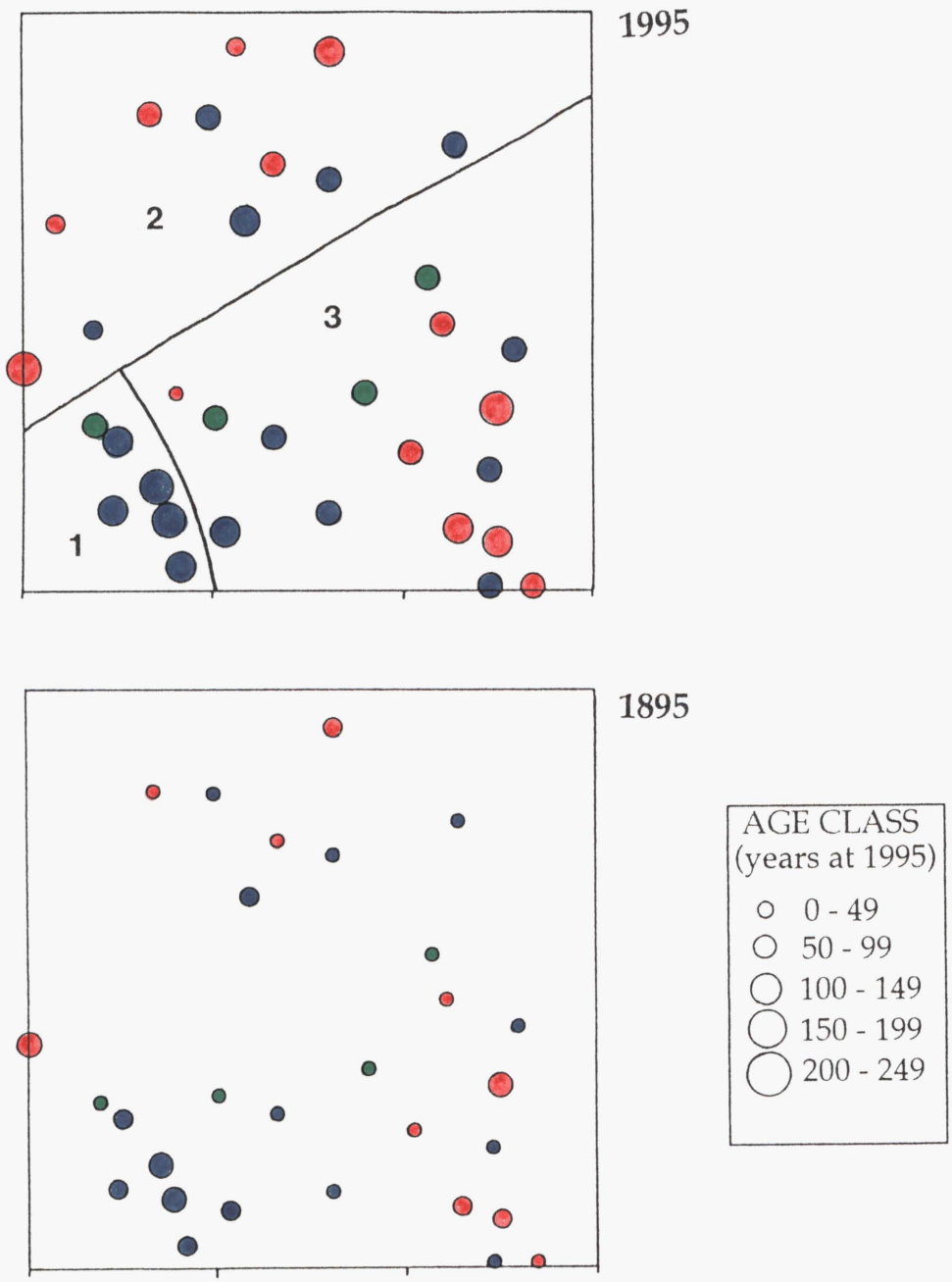
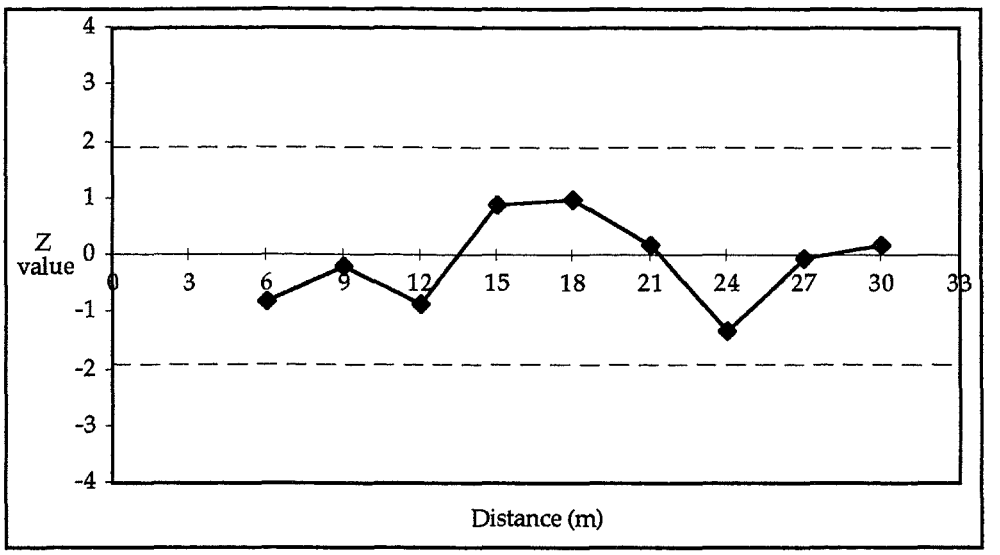


Figure 8.11 Dennistoun Bush Scenic Reserve 2 spatial description.

A. PLOT MAP (age).



B. SPATIAL CORRELOGRAM.

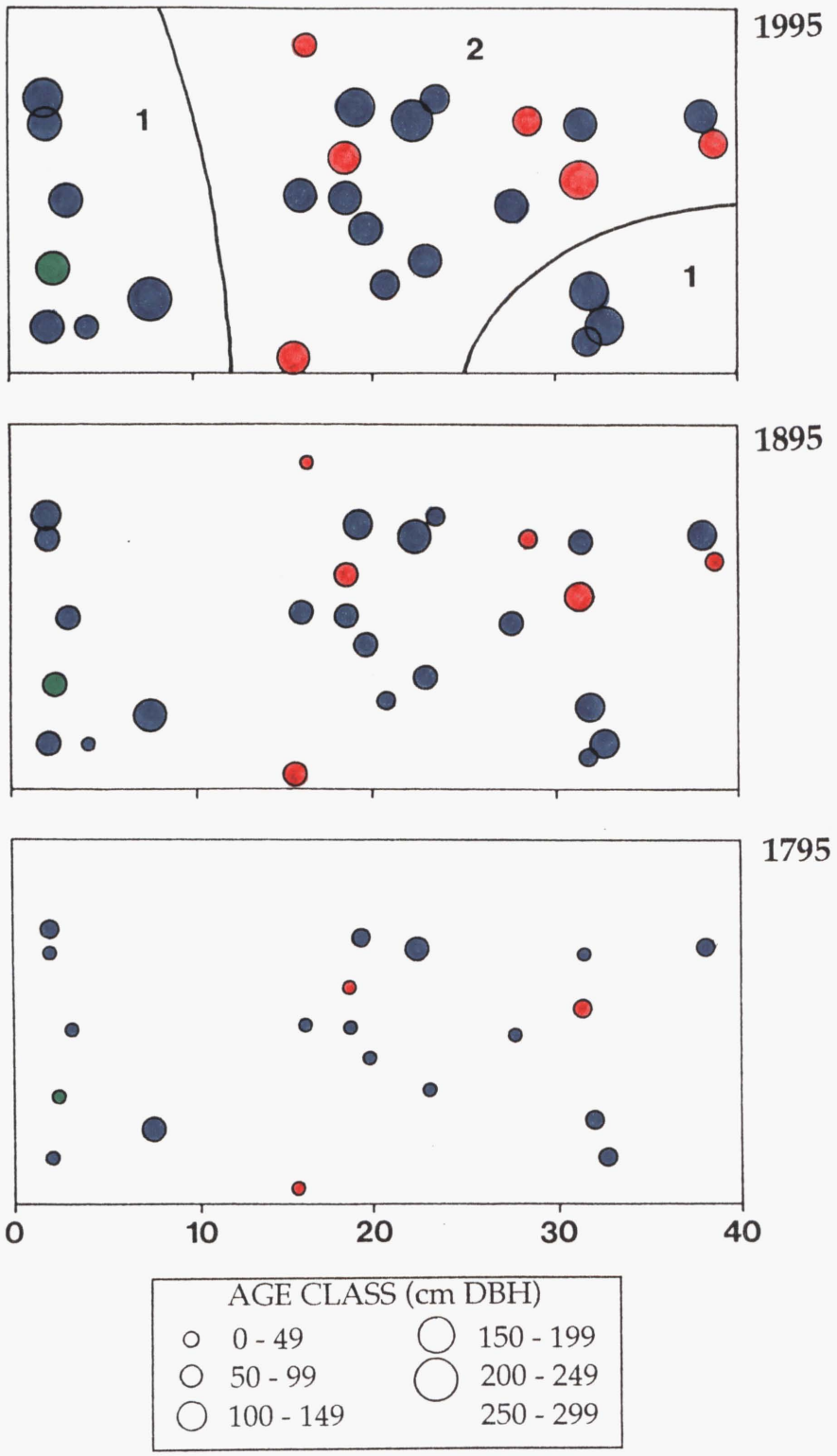


Dennistoun Bush Scenic Reserve 2 (Fig. 8.11) occurs on an active alluvial fan and is classified as totara/matai/kahikatea. This plot contains even-aged trees (Fig. 8.11B) with totara and kahikatea having the widest age ranges (180 and 132 years respectively). Matai has the most limited age range (38 years) and enters the stand after the other podocarps.

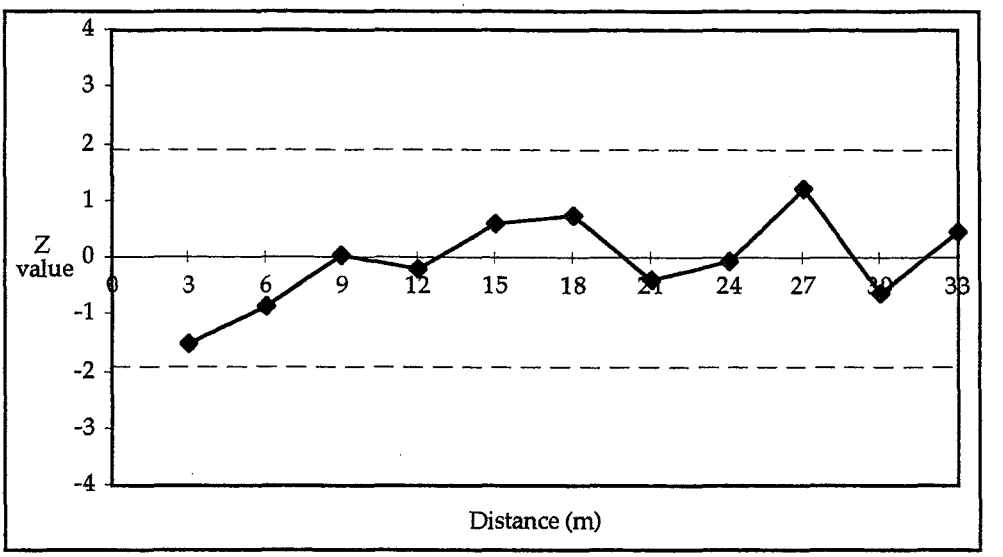
While this stand is shown to be even-aged (spatial autocorrelation), spatial analysis (Table 8.2) indicates clumping of totara at 8m distances and kahikatea 6m.

Figure 8.12 Dennistoun Bush Scenic Reserve 1 spatial description.

A. PLOT MAP (age).



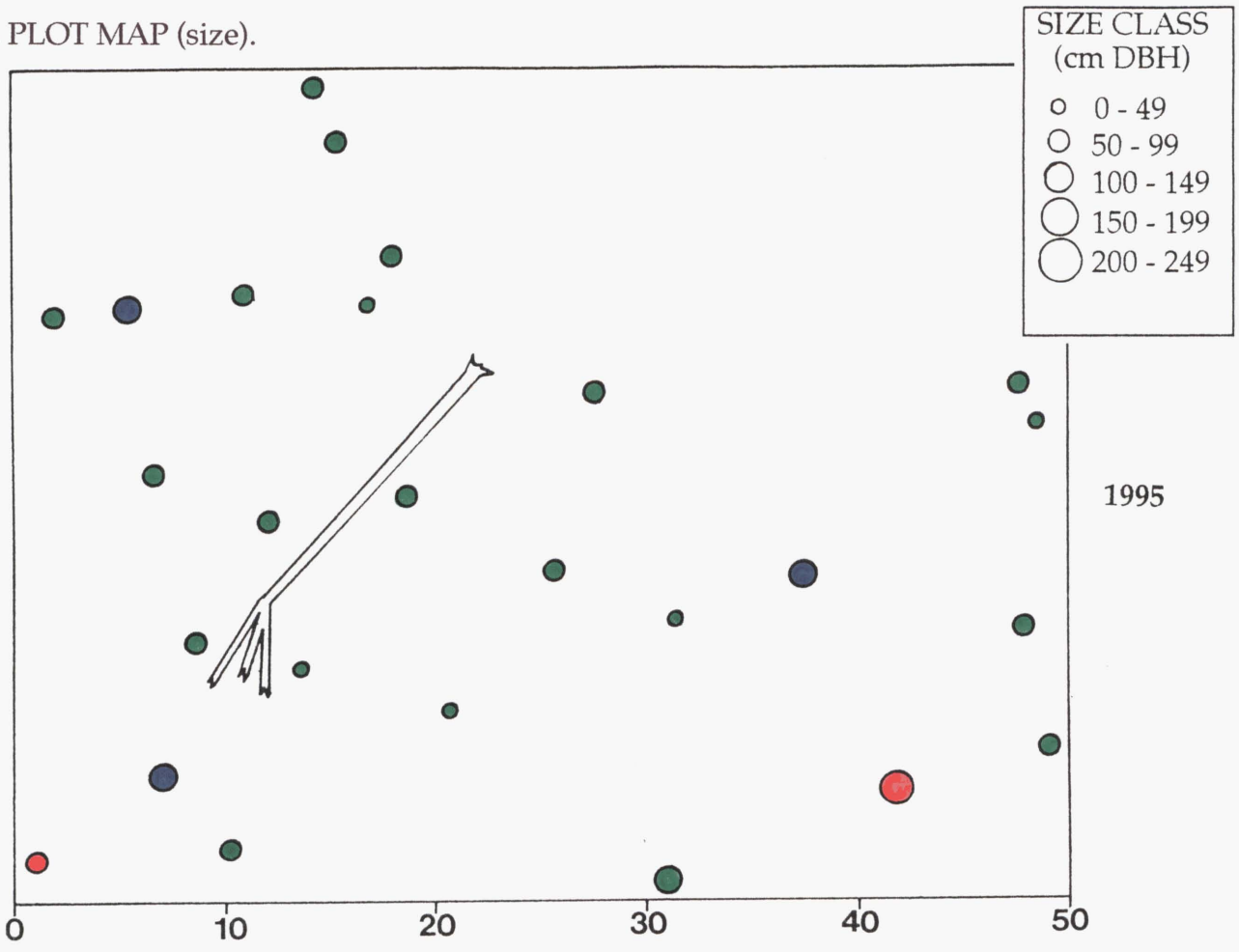
B. SPATIAL CORRELOGRAM.



Dennistoun Bush Scenic Reserve 1 (Fig. 8.12) occurs on the same active alluvial fan as Dennistoun Bush 2 and is also classified as totara/matai/kahikatea. This plot also contains even-aged trees with totara and kahikatea having the widest age ranges (123 and 175 years respectively). Matai has the most limited age range (one adult at 240 years old) and entered the stand after the other podocarps.

Figure 8.13 Price's Valley Covenant spatial description.

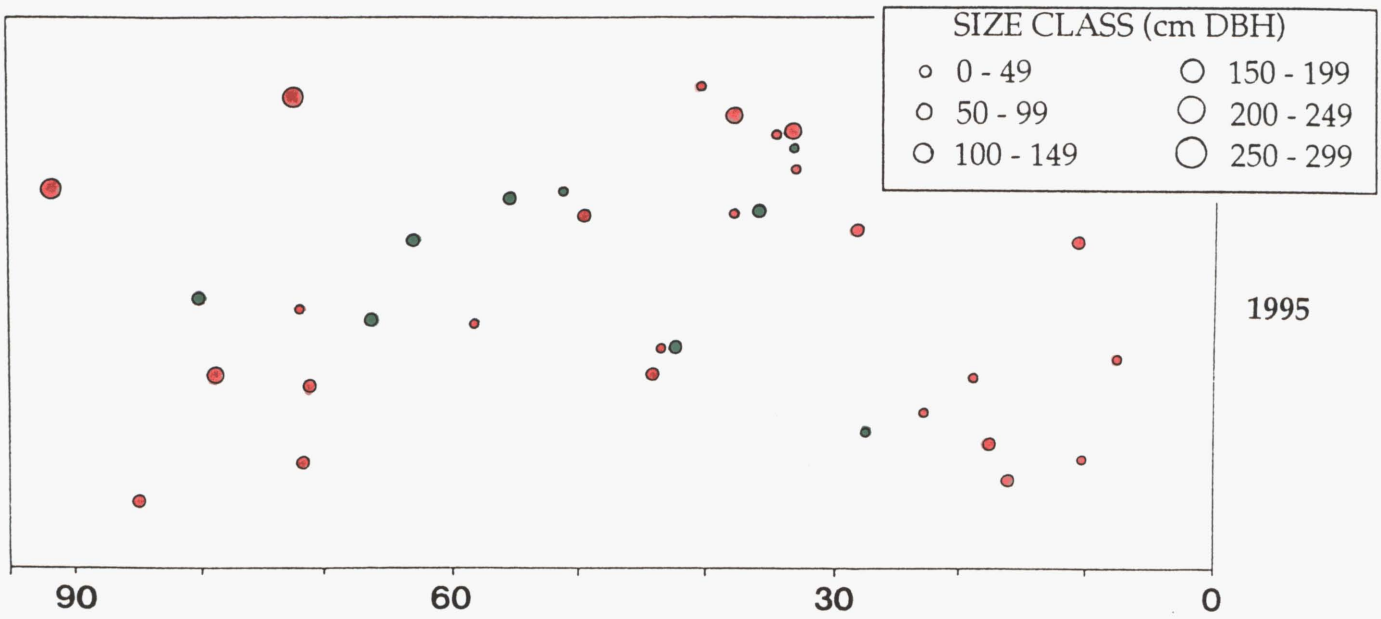
A. PLOT MAP (size).



Price's Valley Covenant (Fig. 8.13) occurs on a river plain and is almost pure matai (see Plate 4). A few large totara and kahikatea occur, as well as seedlings of all three species. The dominant subcanopy angiosperm is titoki which indicates disturbance, most likely from flooding or forest clearance. The predominantly large size of the podocarps excluded this stand from ageing. Size class frequency distribution (Fig. 6.14) shows a limited size range for matai. One large totara occurs (>160cm D.B.H.).

Figure 8.14 Peraki Saddle Scenic Reserve spatial description.

A. PLOT MAP (size).



Peraki Saddle Scenic Reserve (Fig. 8.14) occurs on a colluvial slope and is classified as totara/matai. Lowland totara is replaced by Hall's totara in the upper reaches and a hybrid group occurs at intermediate altitudes. Lowland totara and matai individuals are large (circa 150cm D.B.H.) and so this stand was not aged. Size class frequency distribution (Fig. 6.15) shows a wide range of sizes.

Figure 8.15 Blue Duck Scenic Reserve 1 spatial description.

A. PLOT MAP (size).

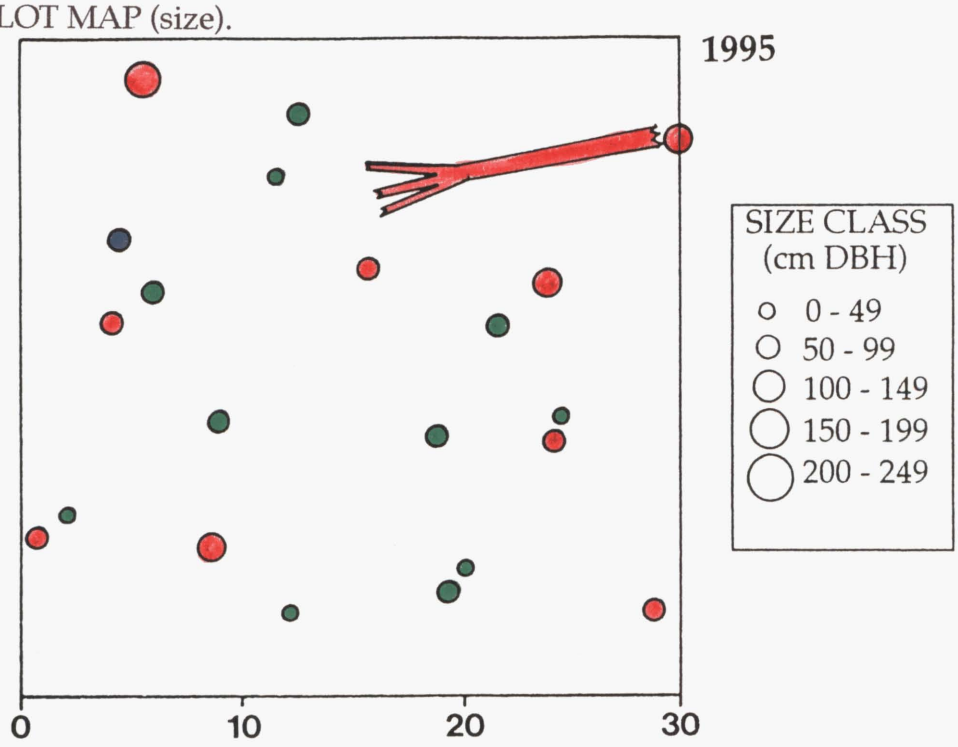
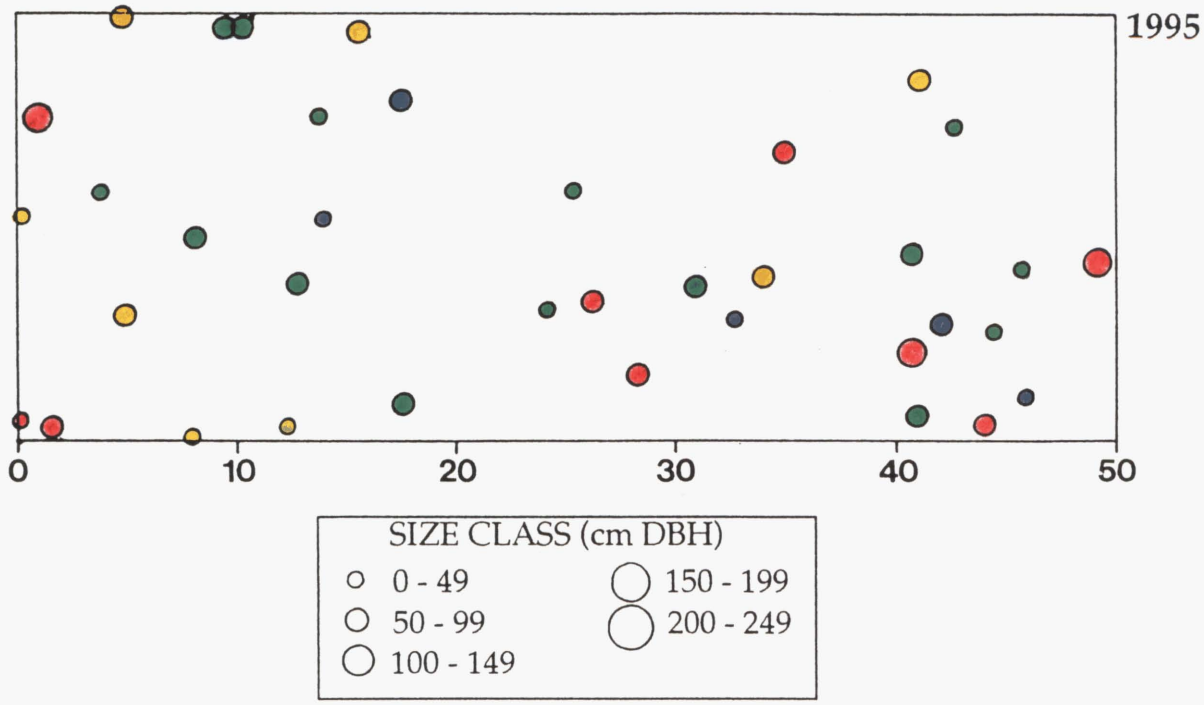


Figure 8.16 Blue Duck Scenic Reserve 2 spatial description.

A. PLOT MAP (size).



Blue Duck 1 (Fig. 8.15) and 2 (Fig. 8.16) occur on colluvial slopes and are classified as dense mixed podocarps. The large size of individuals meant that absolute age determinations were too inaccurate to be used in age class distributions. Size class frequency distributions (Fig. 6.16 and 6.17) shows a wide range of sizes, suggesting that these stands are not even-aged.

In both Big Tree and Denn Huge, only trees greater than 50cm D.B.H. were recorded. Big Tree, Peel Forest (Fig. 8.17) occurs on an alluvial terrace and is classified as totara/matai/kahikatea. The large size of the trees (circa 160cm D.B.H.) excluded this stand from ageing. Dennistoun Bush Huge data are from three adjacent plots (Fig. 8.16) which occur near Denn Bush 1 and 2. This stand has not been disturbed recently and large totara individuals (circa 250cm D.B.H.) occur as emergents above matai and kahikatea. Size class frequency distributions (Fig. 6.18 and 6.19) shows a wide range of sizes, suggesting that these stands are not even-aged.

Figure 8.17 Big Tree Peel Forest stand growth.

A. PLOT MAP (size).

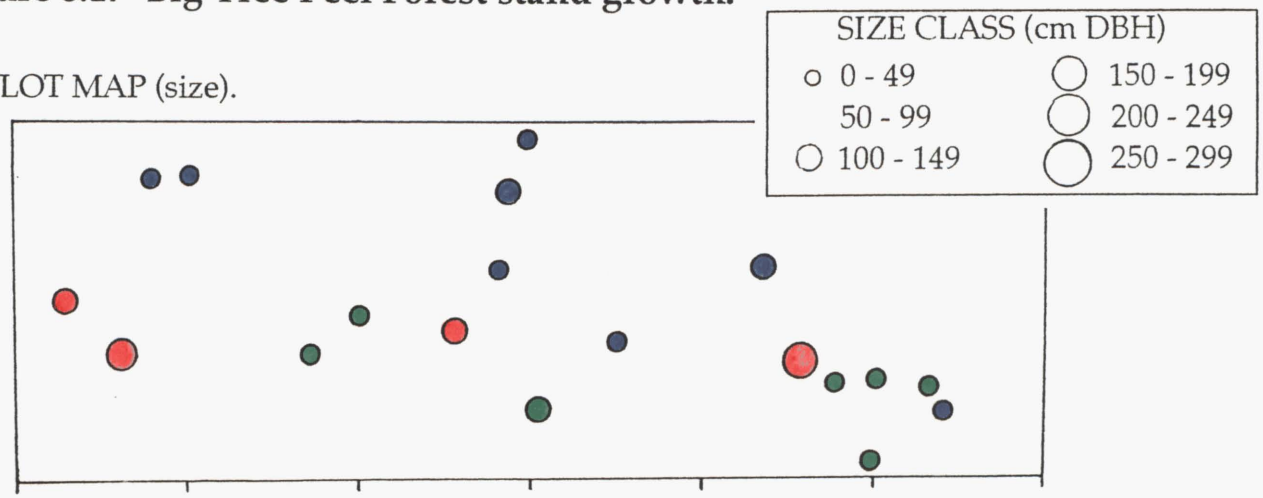
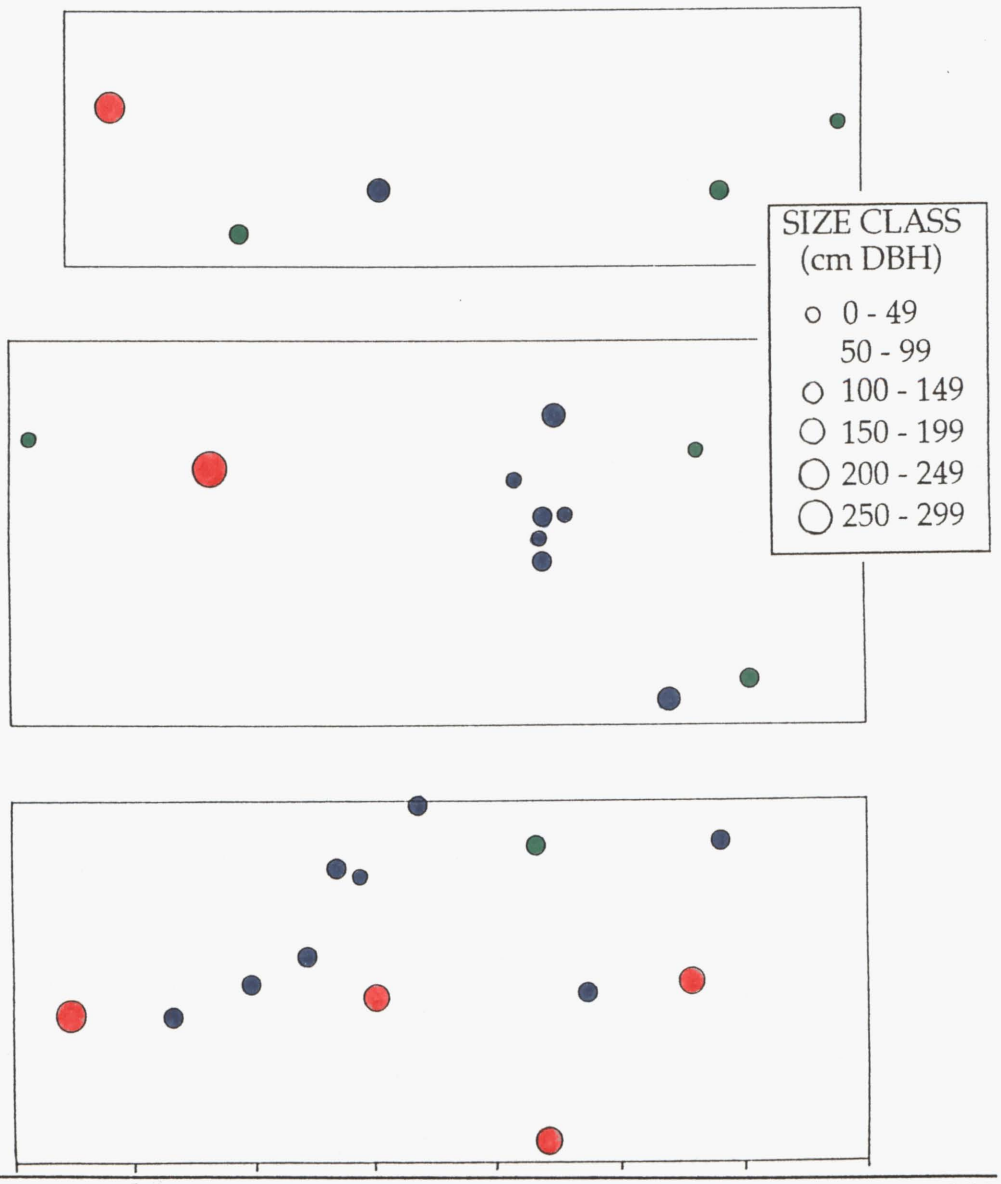


Figure 8.18 Dennistoun Bush Huge stand growth.

A. PLOT MAP (size).



8.4 DISCUSSION

While sample sizes are small for many stands, some results are discernible. ANOVA shows that the three main podocarp species exhibit different spacing. Totara shows a significant correlation between mean spacing and mean size, and mean spacing and number of adult stems. This indicates the numerical dominance of lowland totara.

• Are adult tree distributed at random? If not, what are the patterns, processes, and associations? Totara and kahikatea show a certain degree of clumping in several stands whereas matai is randomly distributed throughout the stands except for in Blue Duck 2. The young/colonising stands of Mananui and Nikau show the most clumped podocarp distributions. Totara is clumped at all distances in Mananui. Kahikatea is clumped in Nikau Reserve at distances up to 6m, suggesting the limitation of this species to its preferred microsites, possibly damp depressions. Spatial distribution of matai is either random or uniform, suggesting that this species is more opportunistic in its capture of sites. Spatial distribution of kahikatea is either clumped or random, suggesting a preference for certain microsites.

Adults of all three podocarp species show an example of repulsion from angiosperms at distances of 3 to 9 meters. In Denn Bush 1, kahikatea shows a repulsion from totara at distances of 6 meters i.e. there are less kahikatea and totara trees spaced at this distance than would be expected under the assumption of random distribution. The totara - matai relationship shows interesting results. Examples of both attraction and repulsion are present, suggesting a unique relationship between these two species.

The main canopy podocarps appear to differ in their relationship with angiosperms depending upon age. Seedlings are attracted to angiosperms (see Table 7.5 and 7.6) which may be a function of dispersal (see Chapter Seven). On the other hand adults are all repulsed from angiosperms, possibly because the angiosperms present when the podocarp adults were seedlings have since died and the podocarps have captured the site. Angiosperms may then establish in gaps between the dominant podocarps. This indicates the fluctuating temporal role of angiosperms within podocarp forest.

• Are the stands even-aged and does this correlate with the disturbance regime? Age ranges of the three main podocarp species is shown in Table 8.5. Maximum

attainable age in the present study is assumed to be approximately 900 years for totara, 800 years for matai, and 600 years for kahikatea. For totara, all of the aged stands except Mananui and Denn Bush 2 shown to be even-aged i.e. most of the aged trees fall into an age range of ten perecent of the maximum attainable range. For matai, all of the stands where this species occurs are considered to be even-aged. For kahikatea, all of the stands where this species occurs except Denn Bush 1 are considered to be even-aged.

Table 8.5 Age range of the podocarps in aged stands (aged from ring counts and estimated from regressions). * = age range less than ten percent of maximum attainable age, ** = 75% or more of the trees have an age range less than ten percent of maximum attainable range.

SITE⇓ SPECIES⇒	TOTARA	KAHIKATEA	MATAI
MANANUI	219	-	-
PUHI PUHI	1*	-	53*
PAYNE'S FORD	55*	-	-
COKE 1	89*	166**	101**
COKE 2	53*	1*	81**
OKUTI VALLEY	102**	-	45*
OKUTI (kanuka)	98**	1*	26*
DENN BUSH 2	180	132**	38*
DENN BUSH 1	123**	175	1*

Spatial autocorrelation analysis also indicates that most stands studied do not contain different patches of even-aged trees. Rather, plots are usually totally within one mosaic patch (see Pickett & White 1979) and contain relatively even-aged trees. Mananui Bush is the largest plot (100 x 50m) and shows the presence of different patches of even-aged trees which have regenerated due to the prograding nature of this dune system.

The majority of young/colonising and mature lowland totara dominated stands are seen to be even-aged, regenerating as a result of medium to catastrophic disturbance which acts to elevate light levels and provide new colonisation surfaces. In the previous chapters, distribution and niche, disturbance history, seedling ecology, and spatial description have been investigated. Stand growth through time is outlined in the next chapter via a study of ring width. Generalised models of lowland totara growth are then presented.

CHAPTER NINE
STAND GROWTH THROUGH TIME

9.1 INTRODUCTION AND OBJECTIVES

In the previous chapters, ecological niche, disturbance history, seedling ecology, and spatial description have been investigated. The role of catastrophic disturbance in the development of totara dominated stands has been determined. Stands have been described in terms of age class, associations, and seedling and adult distribution. Spatial descriptions show most stands to be even-aged, regenerating in response to medium to catastrophic disturbance. In order to determine the future development of totara dominated stands, and to develop a generalised model of stand development, stand growth through time requires further investigation.

The objectives of this chapter are:
- To investigate stand growth through time via a study of mean ring width.

To fulfill this objective, the research questions are addressed:
- Does lowland totara dominated forest develop along a predictable pathway of stand growth?
- If so, can models be generated to aid in predicting the future development of lowland totara dominated stands?

9.2 METHODS

Stand growth through time is presented as mean ten year ring width i.e. assumed to be approximately half of the annual diameter increment. Annual ring width was recorded during ring counting and averaged every ten years. Where two cores per tree were counted, the mean of the ten year mean ring widths and standard deviations of the two cores is presented. Where only one core per tree was counted, only this core is presented. Standard deviations are presented for all mean 10 year ring width measurements.

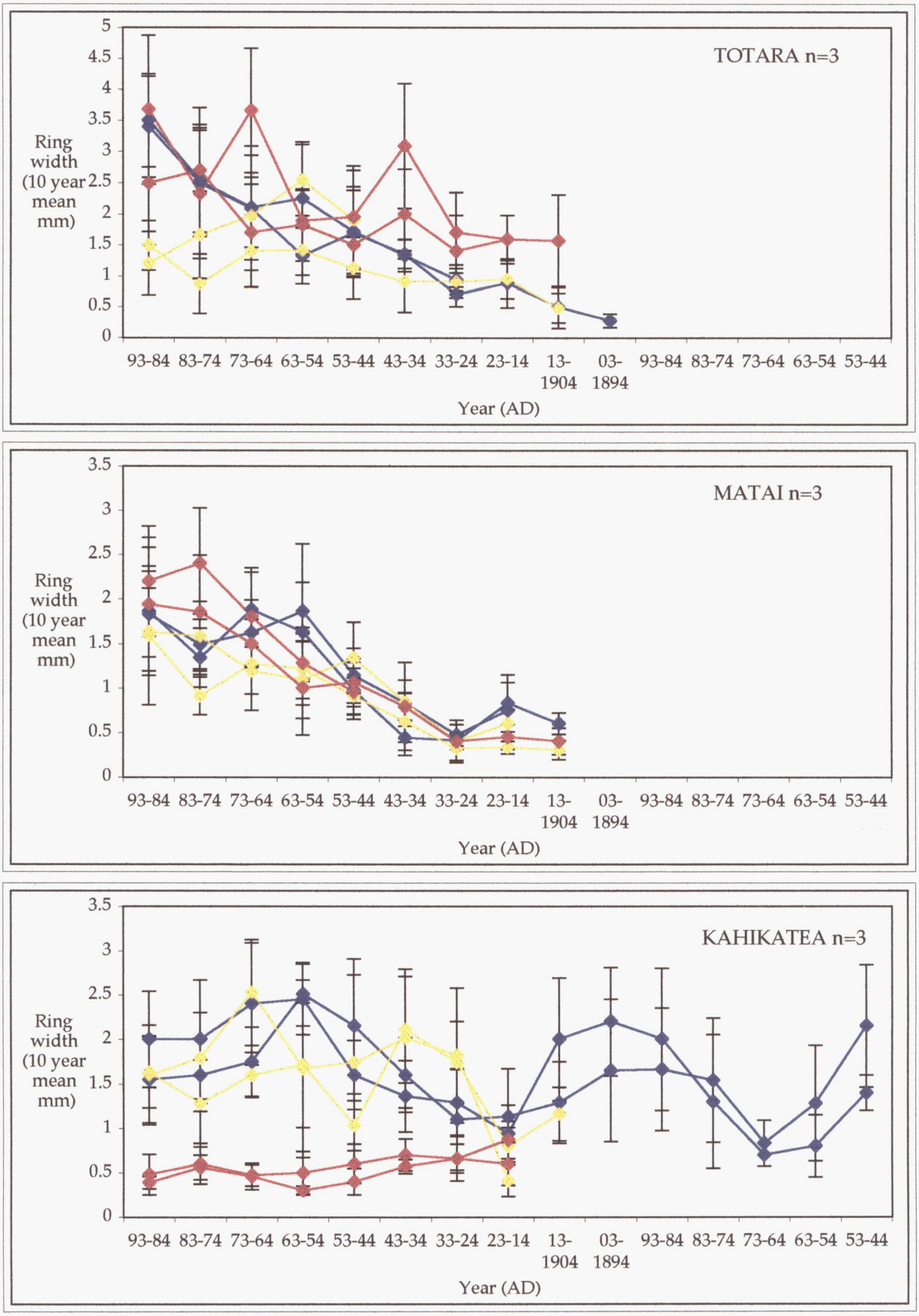
The mean of two cores is presented so as to reduce ring width variation and some of the error involved with missing rings or lobate growth (Fritts 1976), and to

eliminate confusion due to excessive points on graphs. Where two cores per tree were collected, cores were taken from opposite sides of the boles so that within-tree variation in ring width could be determined. Figure 9.1 shows ring width through time of two cores collected from randomly selected trees of totara, matai, and kahikatea. Trees appear to show constant variation in ring width around the bole, indicating that within-tree ring width variation is less than ring width variation through time. The use of the mean of two cores therefore accurately shows individual tree growth through time.

Due to the large number of cores collected, mean ring width through time is presented in groups of trees within each study plot. These groups are selected to represent groups of trees which show either similar growth patterns or otherwise elucidate stand growth. Group numbers appear on the plot maps presented in Figures 8.3 to 8.18 in the previous chapter. Sections 3.3.2 and 8.2.1outline the plot map methods.

Several studies show that diameter growth can be correlated with height growth, basal area, and crown width (Dawkins 1963, Leech 1984, Farr et al 1989, Battin 1993). Leech (1984) shows that for *Pinus radiata*, crown width is linearly related to tree diameter at breast height. Farr et al (1989) found that for western hemlock and Sitka spruce both height-diameter and crown width-diameter were positively correlated, although sites varied. Battin (1993) found that rimu had a stronger relationship between crown area and basal area than kamahi, quintinia, and beech. In the present study an assumption is made that measures of ring width equal general tree growth i.e. higher ring width growth rates are assumed to indicate faster height growth rates.

Figure 9.1 Ring width through time of two cores collected from randomly selected trees of totara, matai, and kahikatea.



9.3 RESULTS

In the following figures stand stand growth through time is shown for all aged plots. All aged stands have been standardised to show growth from 1993 back through time. Data from Blue Duck Scenic Reserve appears as stand growth through time (last 300 years) but not as age class distributions due to the large error involved in ring counts of these older trees. In order to extrapolate future stand development, generalised growth models are presented based on the ring width figures. The general colour scheme is again adopted for consistency and ease of graph interpretation: totara (red), matai (green), kahikatea (blue), miro (pale yellow), rimu (yellow).

Figures of stand development and growth through time appear in the following order:

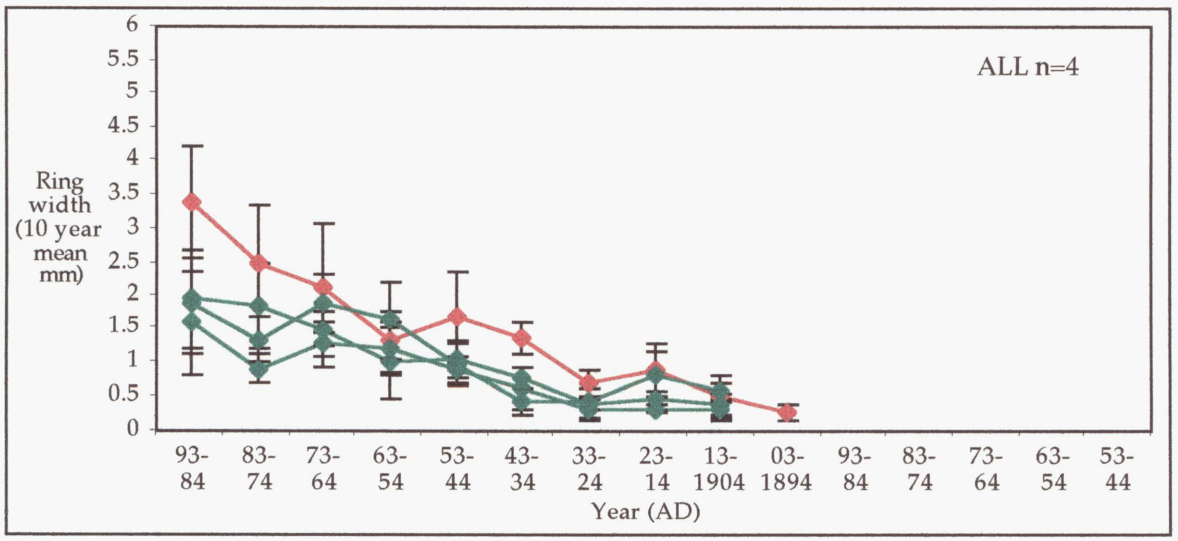
9.3.1 Young/colonising
- Puhi Puhi Scenic Reserve (Fig. 9.2).
- Mananui Bush Scenic Reserve (Fig. 9.3).
- Nikau Scenic Reserve (Fig. 9.4).

9.3.2 Developing stands
- Payne's Ford Scenic Reserve (Fig. 9.5).
- Coke Covenant 1 (Fig. 9.6).
- Coke Covenant 2 (Fig. 9.7).
- Okuti Valley Scenic Reserve (Fig. 9.8).
- Okuti Valley Scenic Reserve kanuka (Fig. 9.9).
- Dennistoun Bush Scenic Reserve 2 (Fig. 9.10).

9.3.3 Mature stands
- Dennistoun Bush Scenic Reserve 1 (Fig. 9.11).
- Price's Valley Covenant (Fig. 9.12).
- Peraki Saddle Scenic Reserve (Fig. 9.13).
- Blue Duck Scenic Reserve 1 (Fig. 9.14).
- Blue Duck Scenic Reserve 2 (Fig. 9.15).
- Big Tree Peel Forest (Fig. 9.16).

9.3.4 Senescent stands
- Dennistoun Bush Huge (Fig. 9.17).

Figure 9.2 Puhi Puhi Scenic Reserve stand growth.



Puhi Puhi Scenic Reserve (Fig. 9.2) is an almost pure matai stand on an alluvial terrace where fluctuating river levels and flood events create new colonisation surfaces. Stand growth shows that the totara and matai saplings and adults are all increasing in growth from the initial regeneration phase. The podocarps are all emergent over a sparse canopy of angiosperms and the high growth reflects the high light levels present.

Figure 9.3 Mananui Bush Scenic Reserve stand growth.

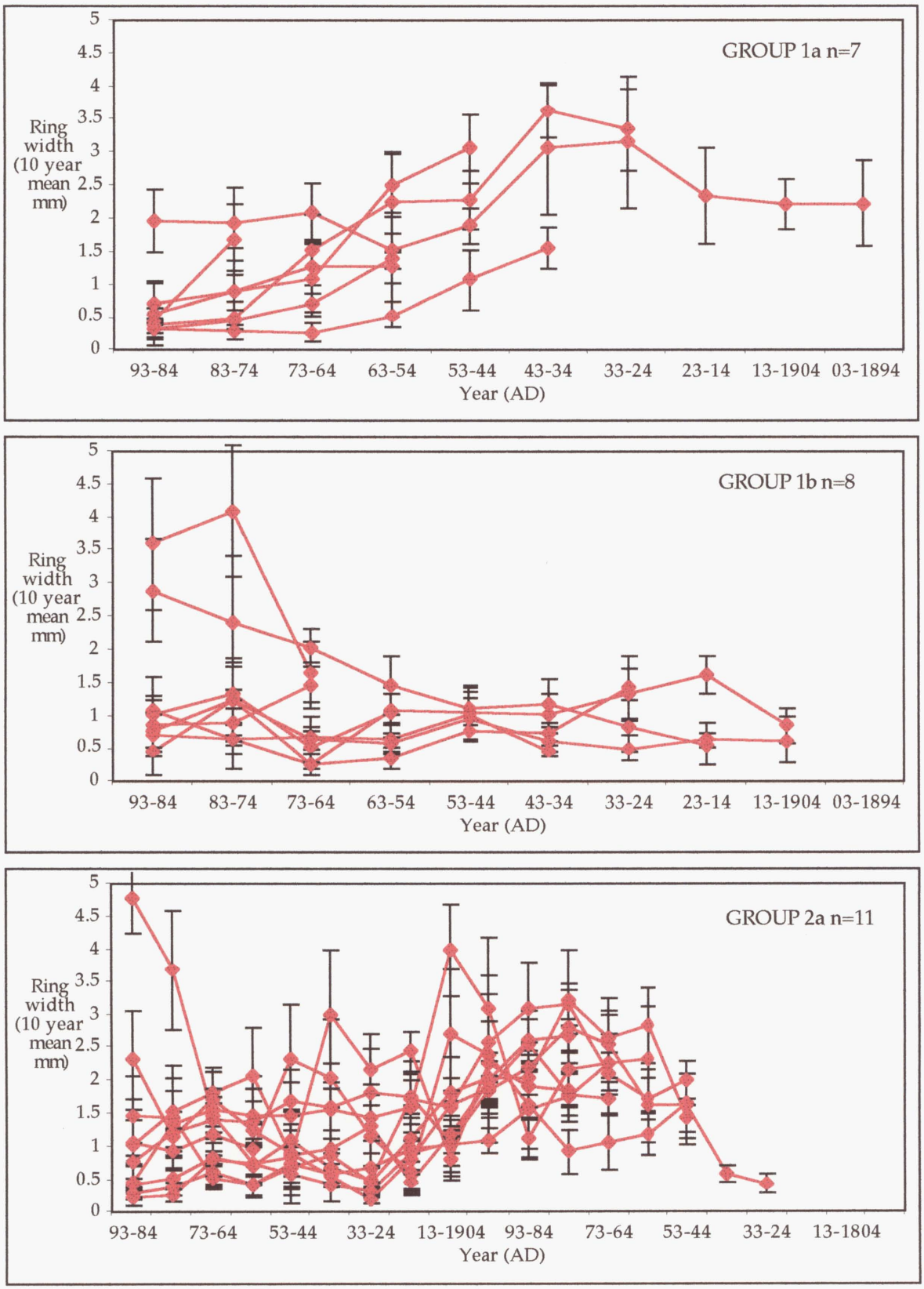
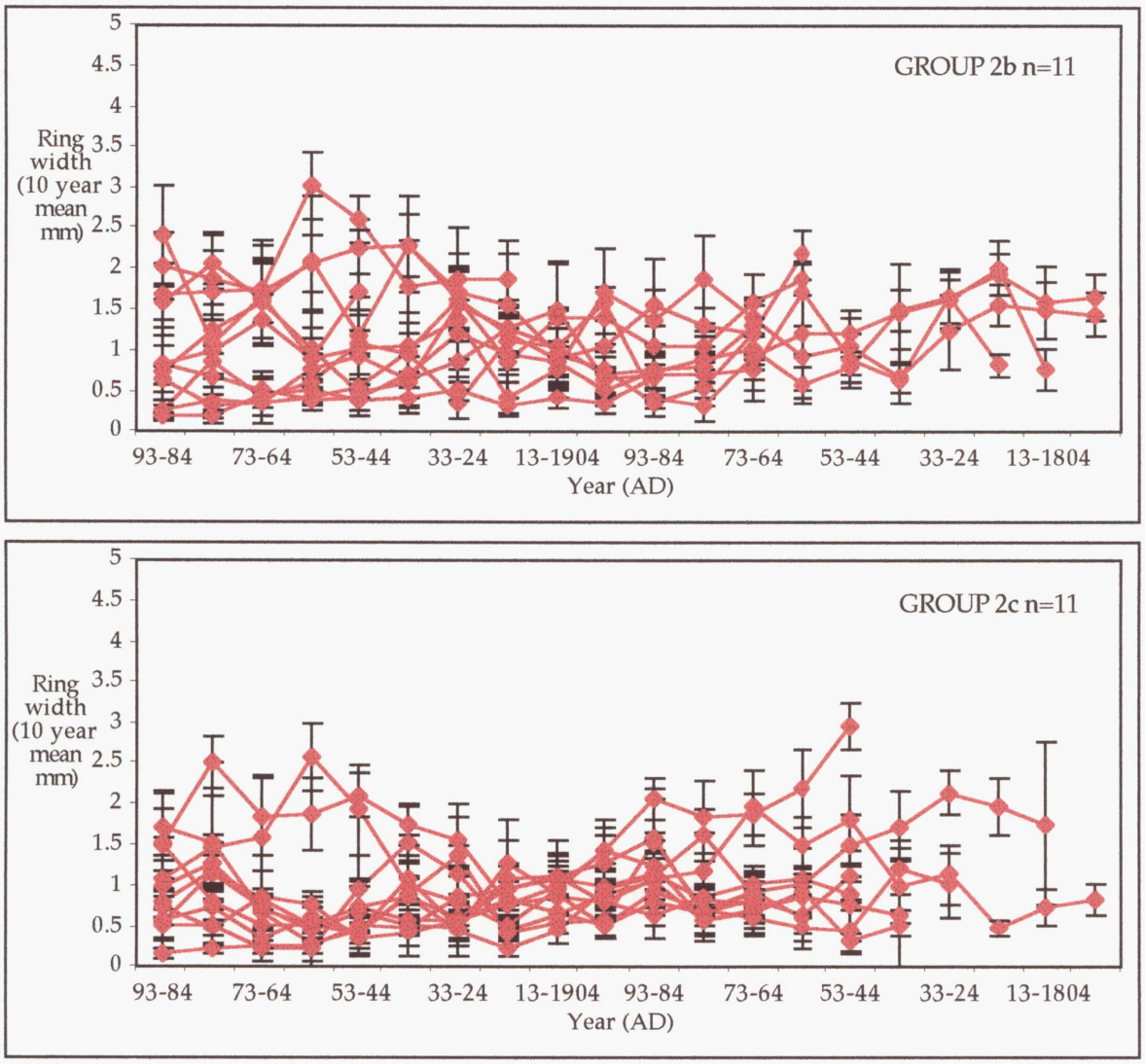


Figure 9.3 Stand growth through time continued.



At Mananui, group 1 (younger patch) shows both suppressed and released individuals (Fig. 9.3). Some individuals show an initial high growth phase and then growth slows, possibly as trees form a closed canopy. Growth is then restricted due to competition. Group 2 (all other trees) shows a similar pattern but canopy closure occurred 100 years ago. Release occurs following windfall of the canopy trees, predominantly on the higher, more exposed, rear dunes.

Payne's Ford Scenic Reserve occurs on a limestone bluff near Takaka and is pure totara (although one matai seedling was encountered). Two large seed trees occur (see Plate 13) and the remaining totara are scattered. The large seed trees are the oldest and show constant growth (Fig. 9.4). Group 3 shows constant high growth. Group 2 shows suppression and recent release. These trees are near the edge of the bluff where a large totara has recently fallen, allowing high light to enter and release the nearby trees. Group 3 shows constant growth.

Figure 9.4 Payne's Ford Scenic Reserve stand growth.

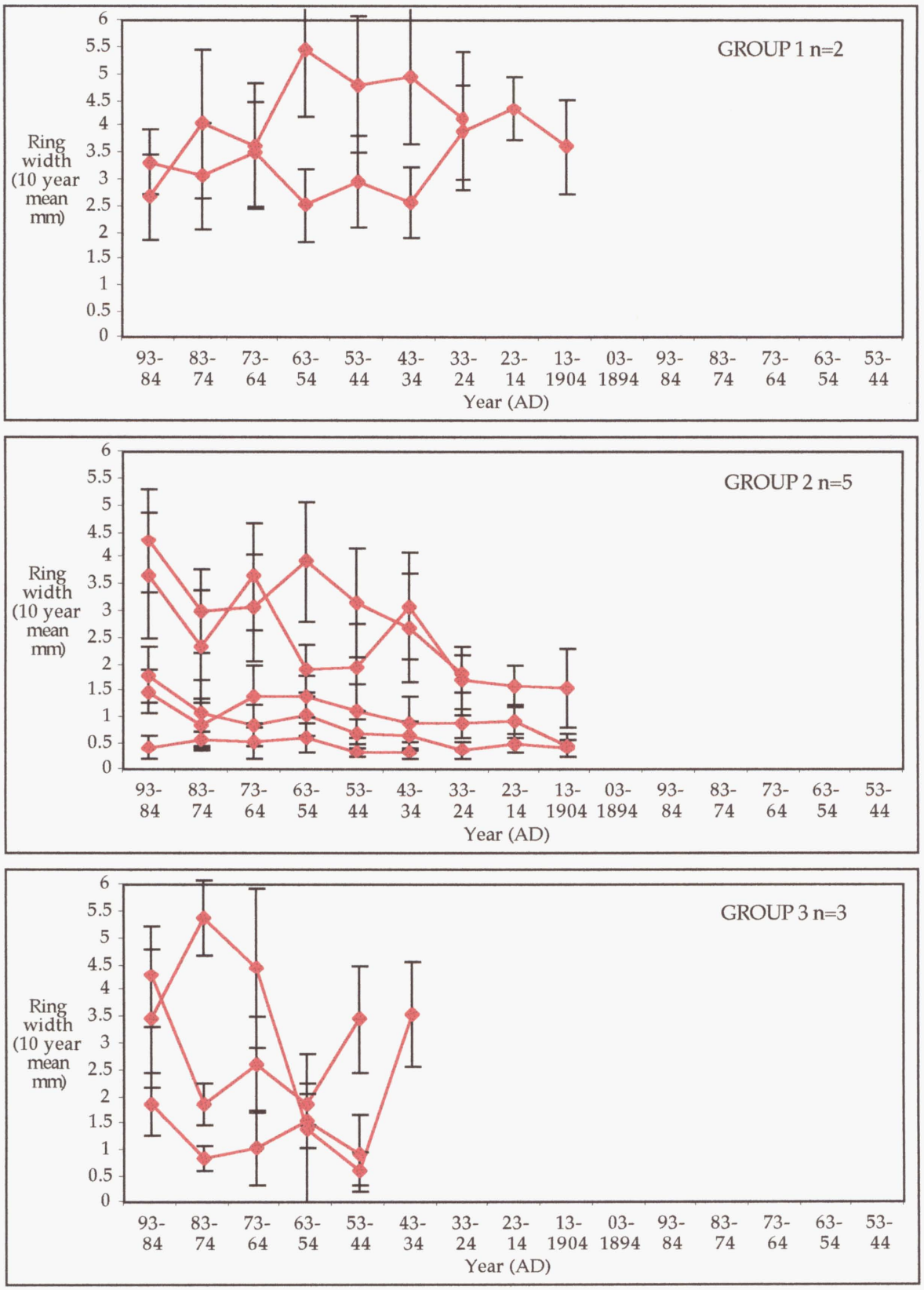


Figure 9.5 Coke Covenant 1 stand growth.

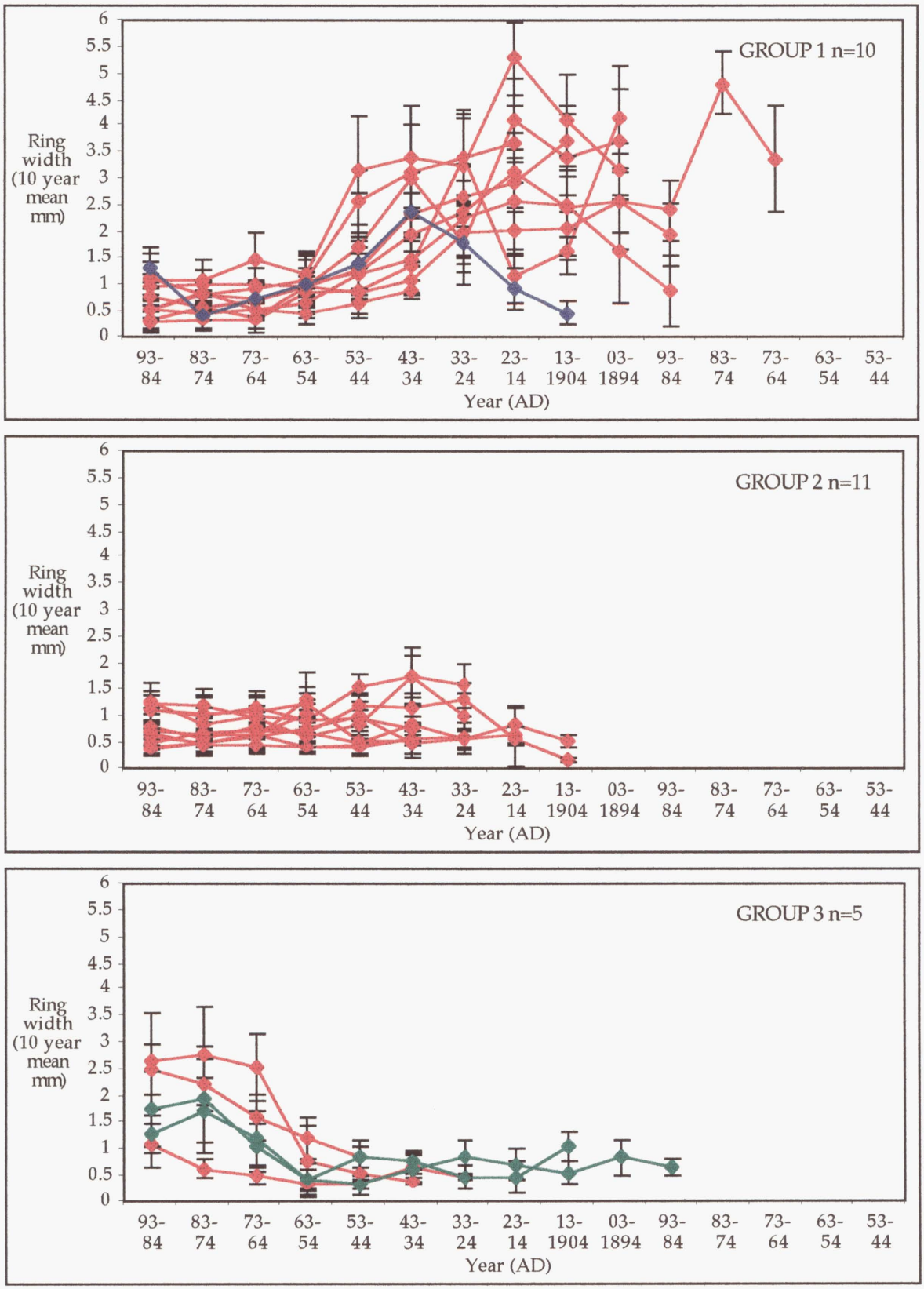
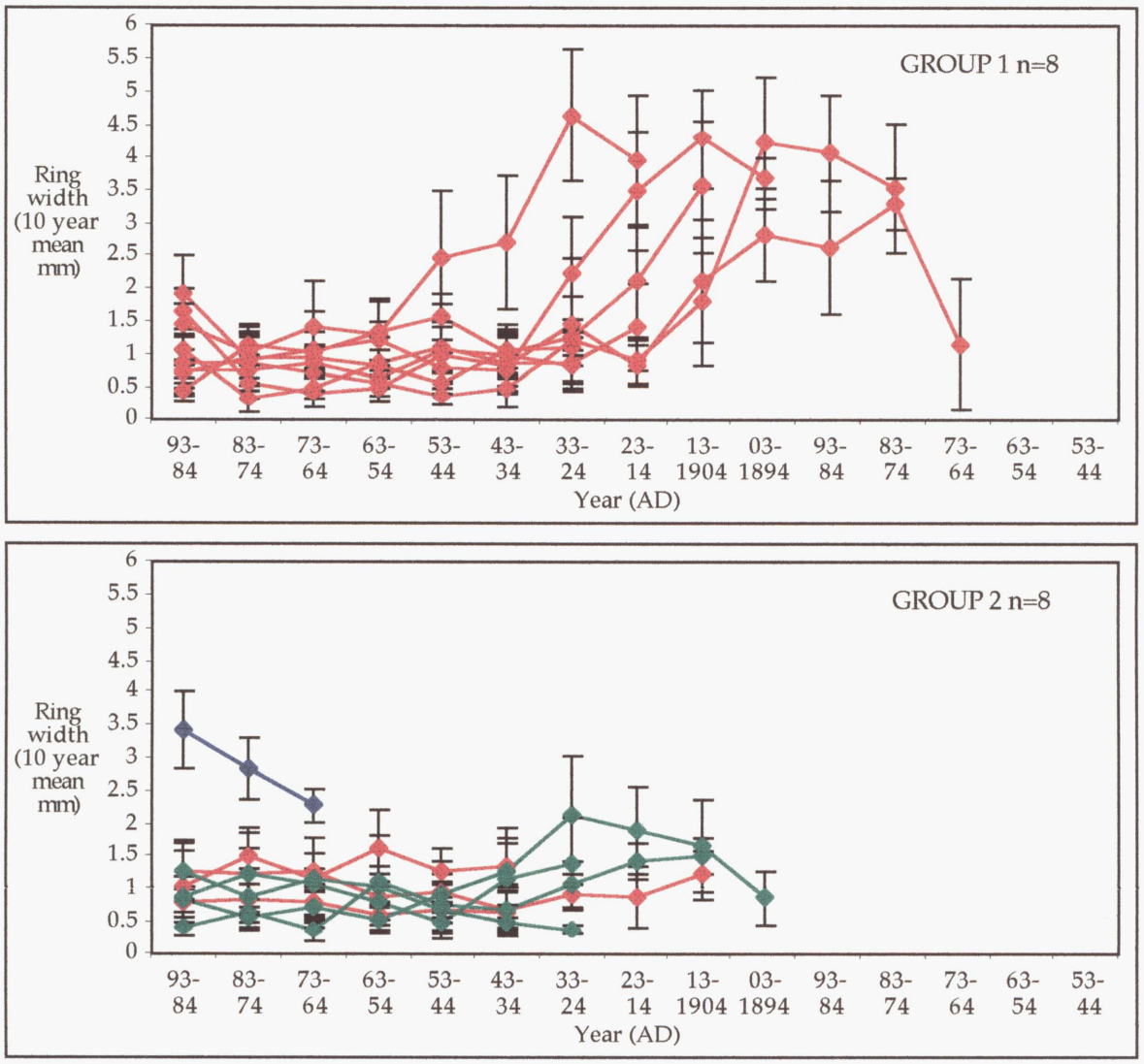


Figure 9.6 Coke Covenant 2 stand growth.



In both Coke 1 and 2, matai shows suppressed growth. Totara trees show either suppression or initial high growth until the canopy closes at approximately 150 years after stand initiation. Both stands have a continuous closed canopy and it appears that totara attains the canopy first through high growth rates, with matai slowly growing to eventually attain the canopy.

Figure 9.7 Okuti Valley Scenic Reserve stand growth.

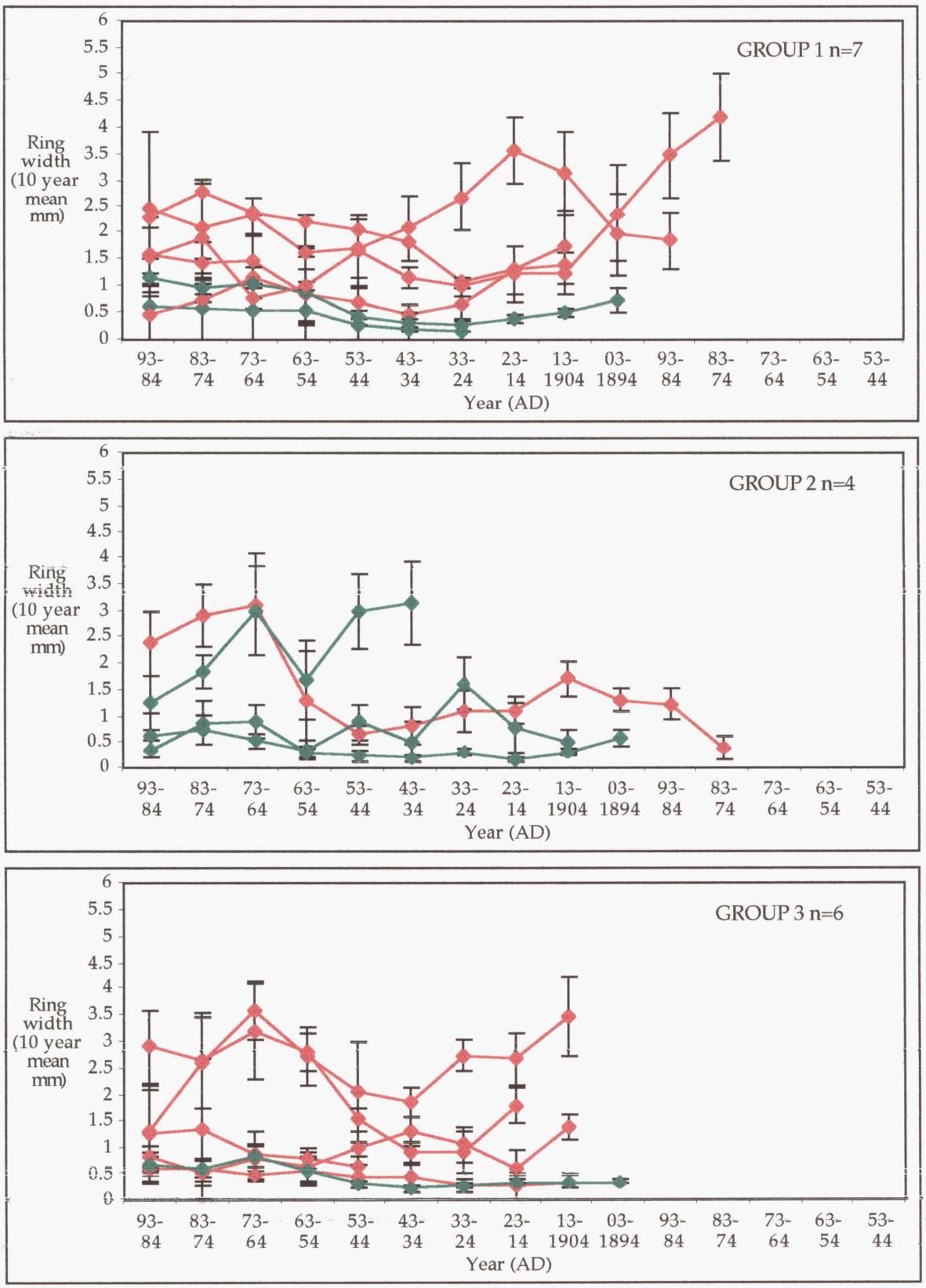
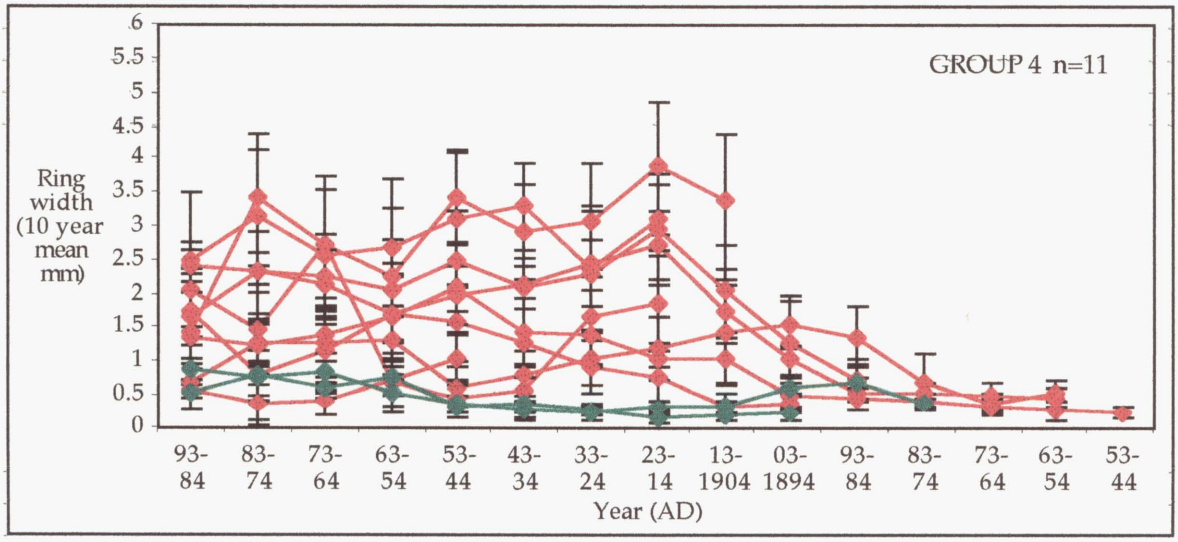


Figure 9.7 Stand growth through time continued.



Okuti Valley Scenic Reserve (Fig. 9.7) and Okuti Valley kanuka (Fig. 9.8) occur on an alluvial terrace within 50m of each other. Both stands show similar age class distributions and stand growth. Fire for forest clearance 150 years ago is the likely stand initiator.

The general trend is for dominant totara individuals with high growth overtopping suppressed totara and matai individuals. Initial high growth of some totara individuals is also seen and canopy closure occurs at approximately 150 years after stand initiation.

Figure 9.8 Okuti Valley Scenic Reserve kanuka stand growth.

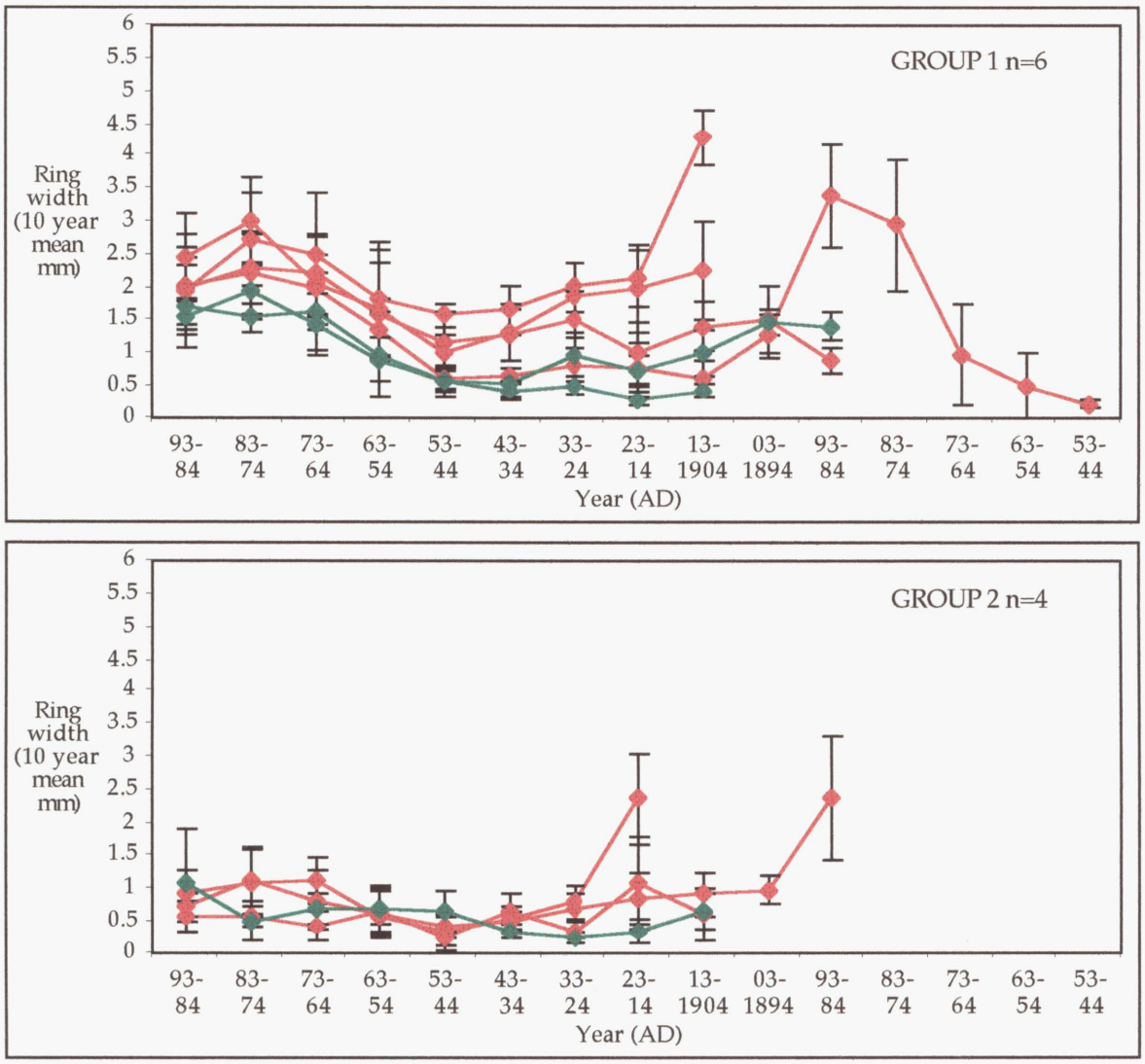


Figure 9.9 Dennistoun Bush Scenic Reserve 2 stand growth.

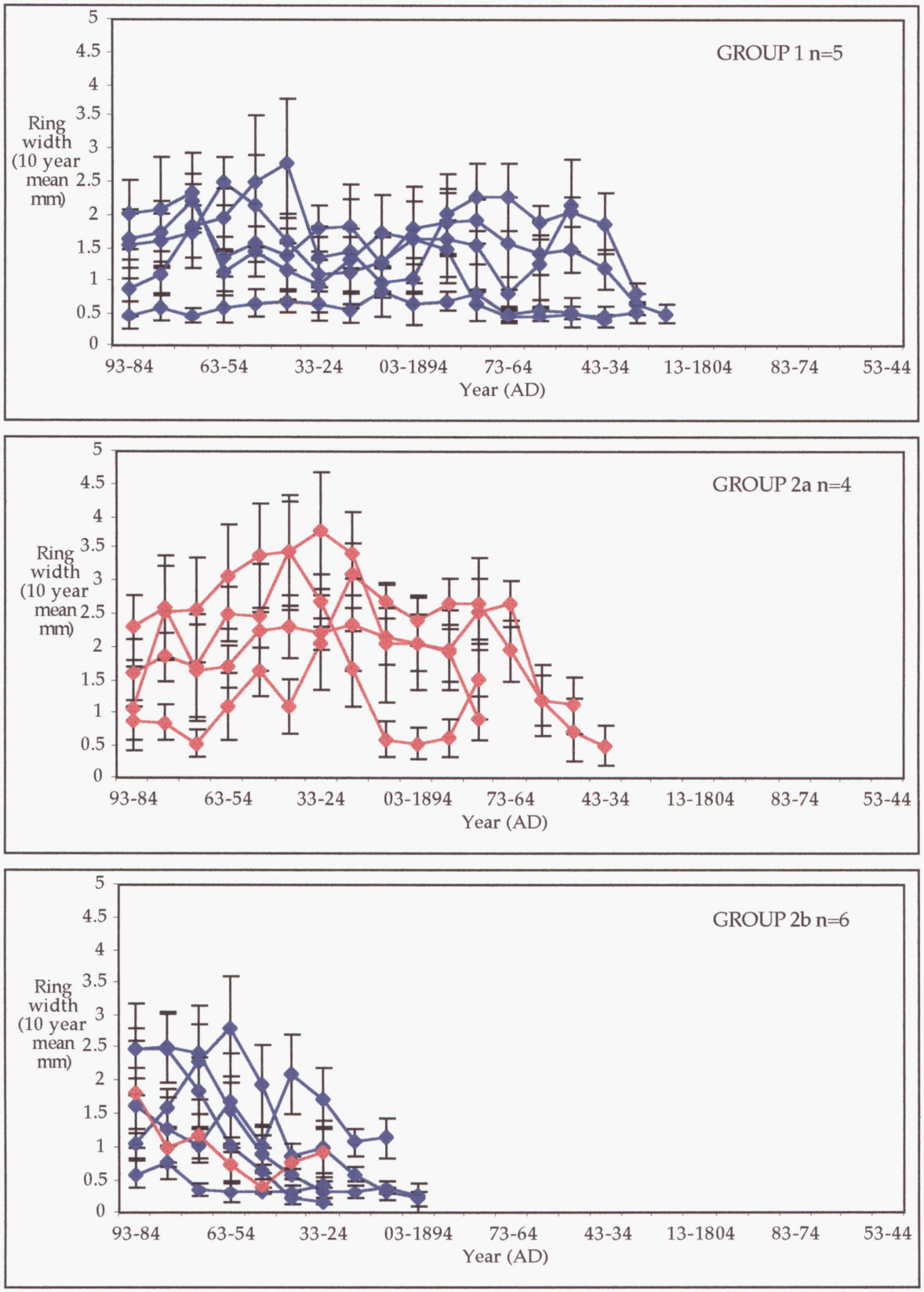


Figure 9.9 Stand growth through time continued.

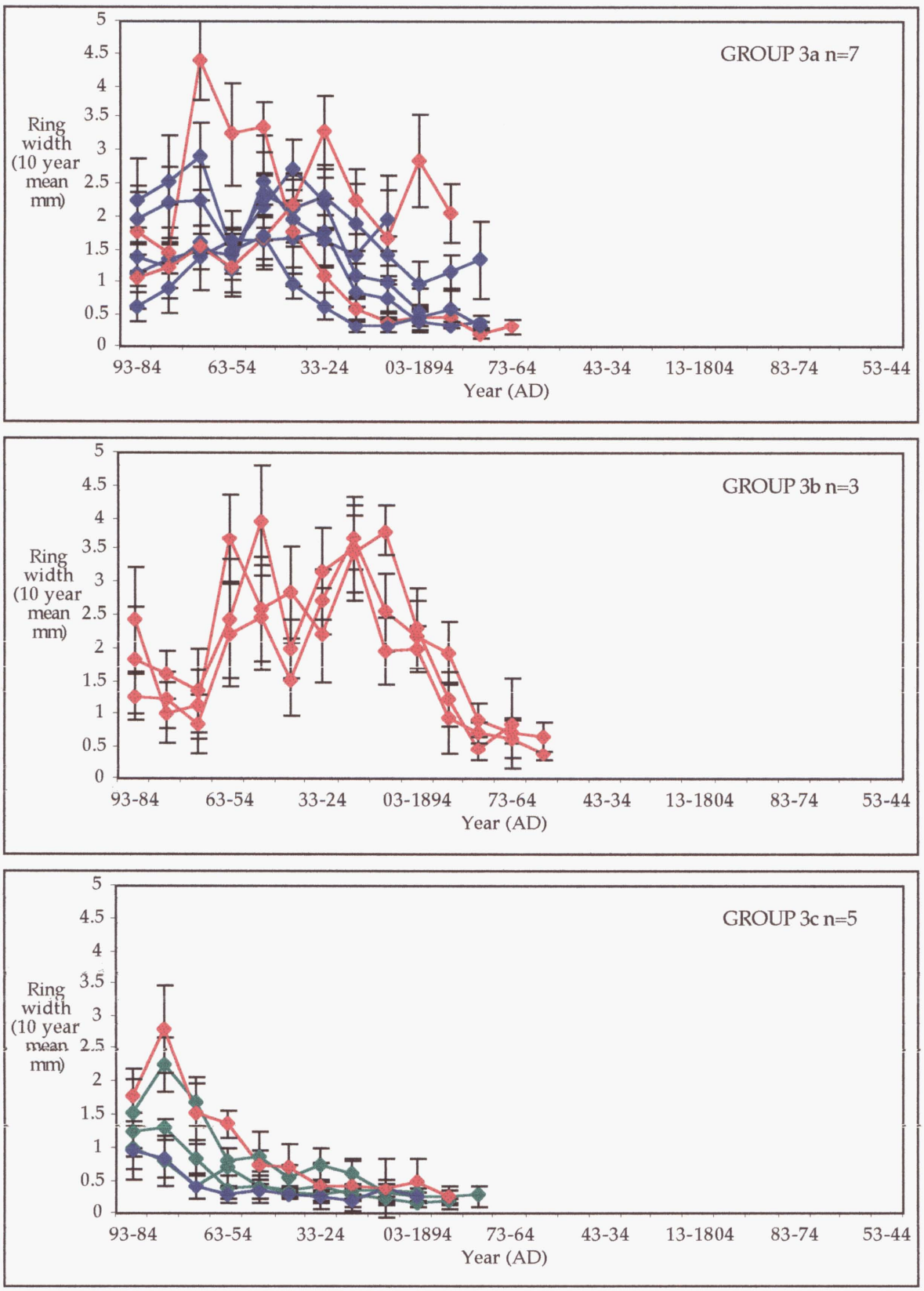
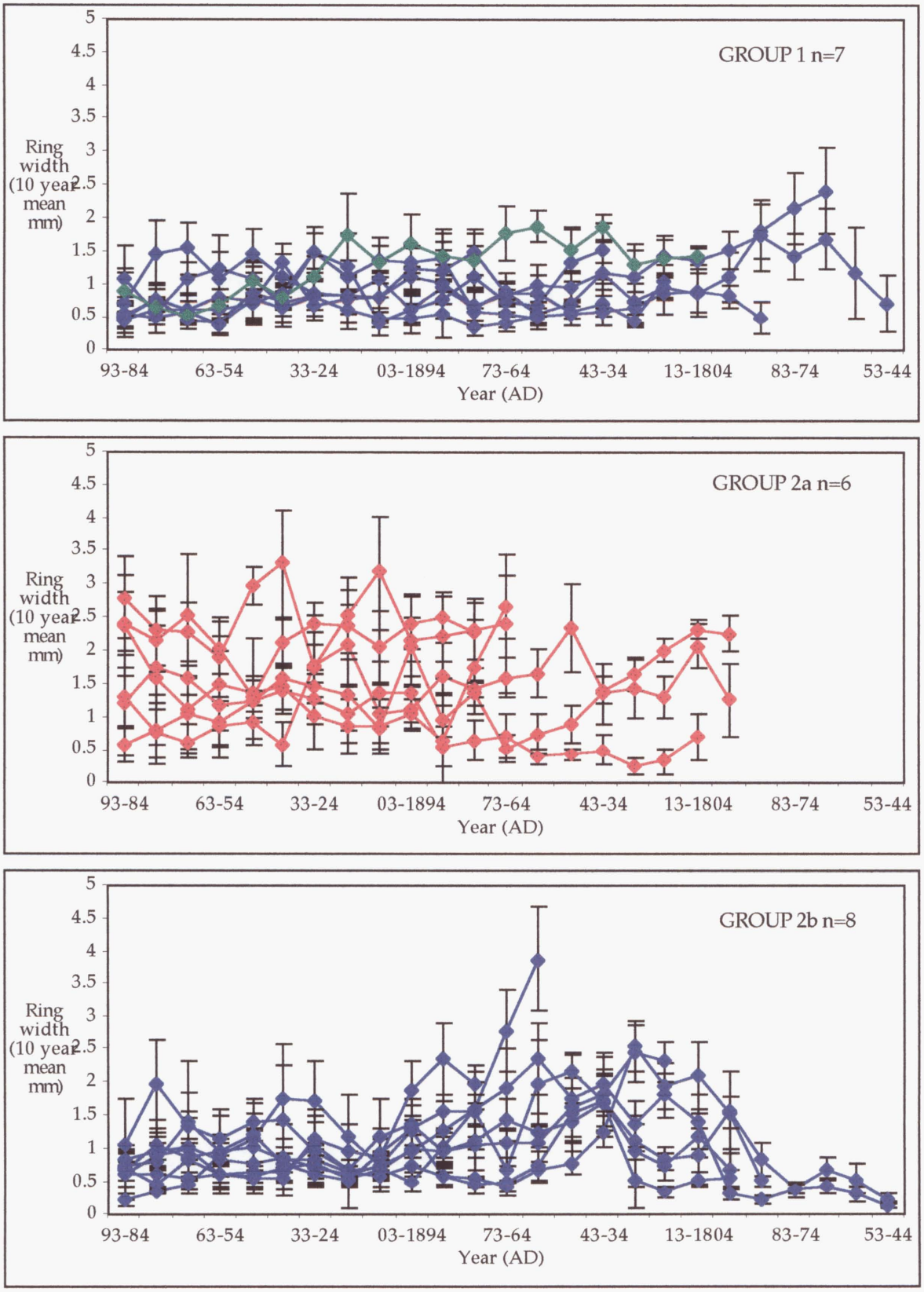


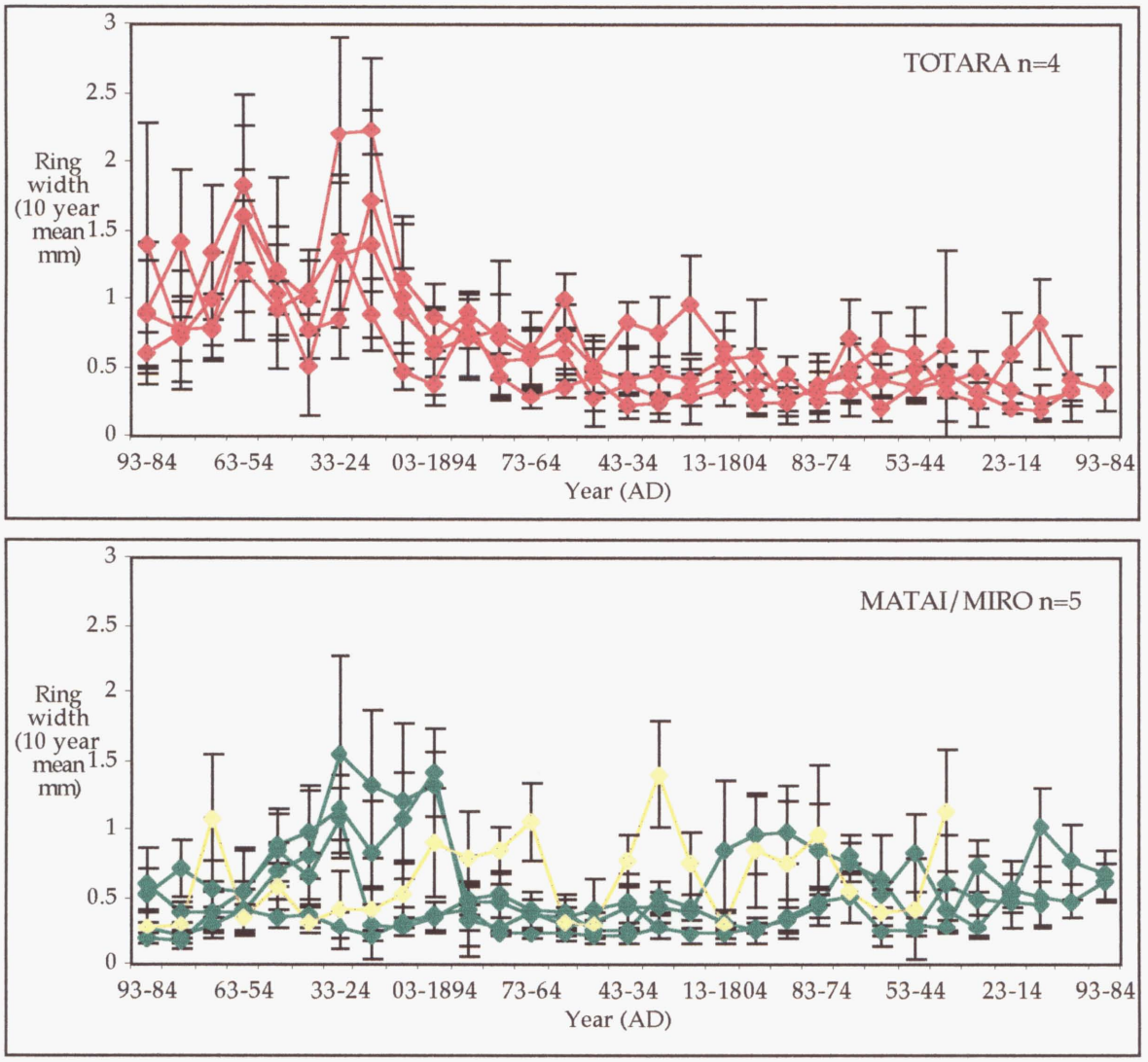
Figure 9.10 Dennistoun Bush Scenic Reserve 1 stand growth.



Diagrams of Denn Bush 1 stand growth through time (Fig. 9.9) show general patterns. Dominant canopy individuals (totara and kahikatea) show high growth until the canopy closes at approximately 180 years after stand initiation. Suppressed totara, kahikatea, and matai individuals occur beneath these dominants. Canopy is mostly closed but somewhat discontinuous, the gaps allowing some individuals to be released.

Diagrams of Denn Bush 2 stand growth through time (Fig. 9.10) show general patterns. This stand is older than Dennistoun Bush 2 and does not contain any seedlings or saplings. Dominant canopy individuals (totara and kahikatea) show initial low growth, possibly under a nurse crop, then high growth until the canopy closes at approximately 200 years after stand initiation. Suppressed totara, kahikatea, and matai individuals occur beneath these dominants. Canopy is continuous and closed, accounting for the present low growth rate of almost all trees in the stand.

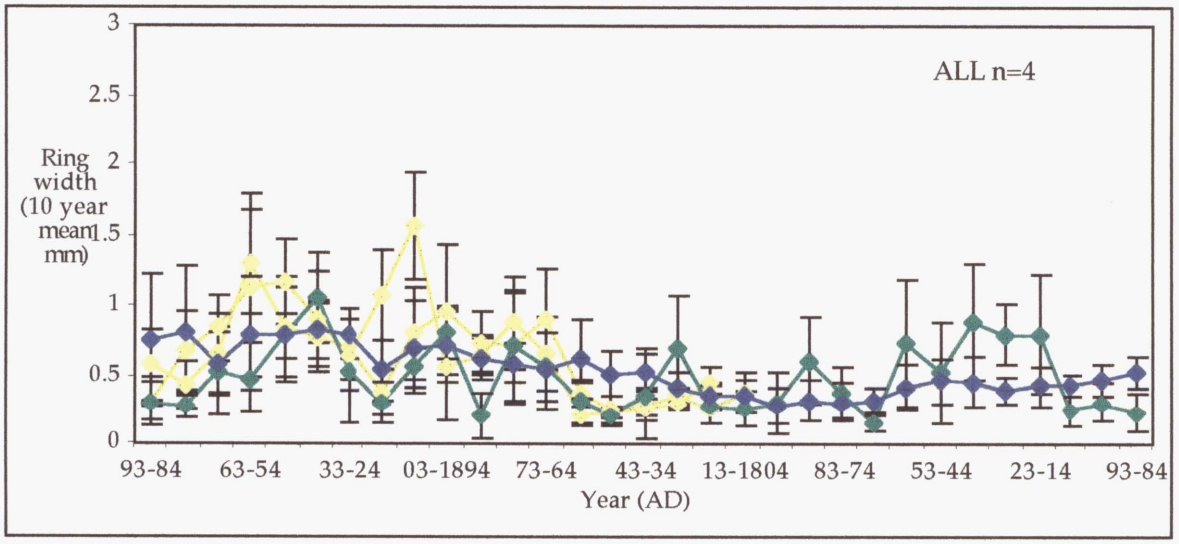
Figure 9.11 Blue Duck Scenic Reserve 1 stand growth.



Both Blue Duck Scenic Reserve 1 (Fig. 9.11) and 2 (Fig. 9.12) occur on colluvial slopes in positions near the ridge tops and are classified as dense mixed podocarps. The large size of the individuals meant that absolute age determinations were too inaccurate to be used in age class distributions. However, stand growth through time is presented as ring counts go back at least 300 years.

Constant low growth rates are shown by all podocarp individuals (Fig. 9.11 & 9.12) until approximately 100 years ago when release occurs. This release may represent individuals becoming emergent from the canopy and hence in high light positions. Growth then slows as the canopy re-closes or the emergents reach the limits of their height growth.

Figure 9.12 Blue Duck Scenic Reserve 2 stand growth.



9.4 DISCUSSION

9.4.1 Diameter growth

Diameter increments per annum for this and other studies appear in Table 9.1. Arlidge (1992) found adult kahikatea males to have consistently wider ring widths than females but this was not statistically significant. Katz (1980b), Herbert (1980), and Bellingham (1980) all recorded ring widths in dense forest and so can be expected to be lower than the maximum found for podocarps in high growth situations e.g. after canopy openings or initial growth to reach the canopy.

Table 9.1 Comparison of mean annual diameter increment range (mm) of the podocarps (adults, present and other studies).

AUTHOR	TOTARA	MATAI	KAHIK	RIMU	MIRO
Present study (min.)	0.4 - 1.0	0.4 - 0.5	0.4 - 0.5	-	0.4
Present study (max.)	3.0 - 11.0	4.0 - 6.0	5.0 - 8.0	-	3.2
Katz (1980b)	-	1.3	2.7	1.6 - 2.1	1.3
Herbert (1980)	-	1.16	-	1.89	1.37
Franklin (1973)	-	-	-	0.3 - 2.5	-
Bellingham (1982)	-	0.51 - 3.77	-	-	-
Arlidge (1992)	-	-	2.78 - 5.92	-	-

In the present study both higher and lower diameter increments per annum than other studies were encountered for adult matai, kahikatea, and miro. No other diameter growth rate data were located for adult totara. The maximum diameter increment found for totara in the present study was 1.1 cm per annum, a rate comparable with more viable silvicultural species e.g. *Pinus radiata*.

9.4.2 Stand development

Stylized diagrams of stand growth, based on mean 10 year ring widths through time, appear in Figure 9.13. Similar patterns of stand development are seen for all stands, regardless of forest type, presence of nurse crop, geographical position, or soil fertility. The regeneration phase lasts 50 - 200 years with totara and kahikatea regenerating first, followed by matai. Young stands show an initial period of high growth until the canopy closes. Stand growth then slows with canopy closure (approximately 180 - 200 years after stand initiation) and maintains a low level of growth until release occurs. It would seem likely that this general pattern is repeated until catastrophic disturbance occurs to re-initiate the stand.

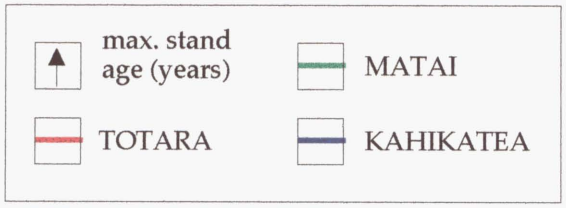
Suppressed individuals, predominantly matai, slowly grow to attain the canopy. Matai is considered to be one of the slowest growing podocarps (Ebbett & Ogden 1998, Beveridge 1974) and most stands containing matai show this constant slow growth pattern.

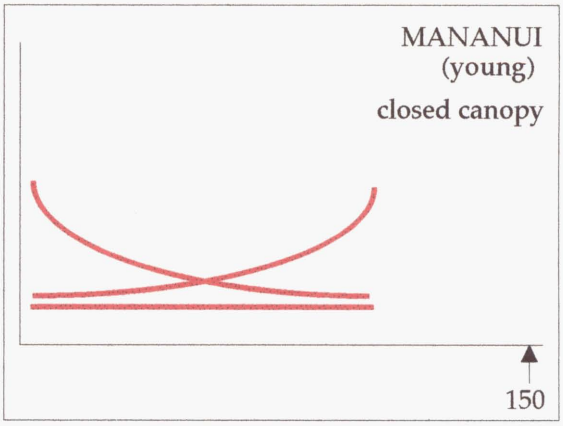
No evidence of generic growth was encountered in the present study, i.e. identifiable growth patterns can not be ascribed to specific diameter classes. Podocarp growth rates depend upon the light environment present rather than tree age or stage of development i.e. high growth corresponds to high light levels. Bellingham (1982) also noted the lack of generic growth in matai.

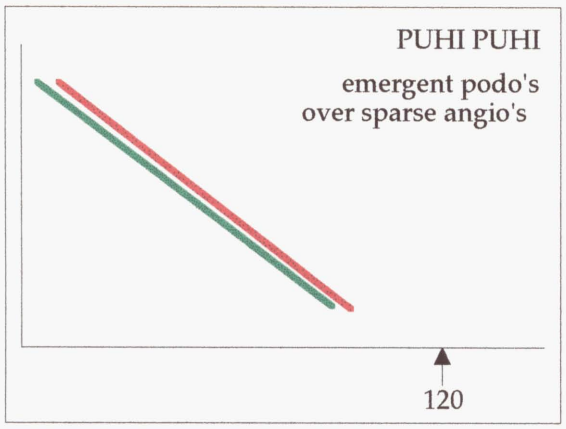
A generalised model of totara-dominated stand growth through time appears in Figure 9.14.

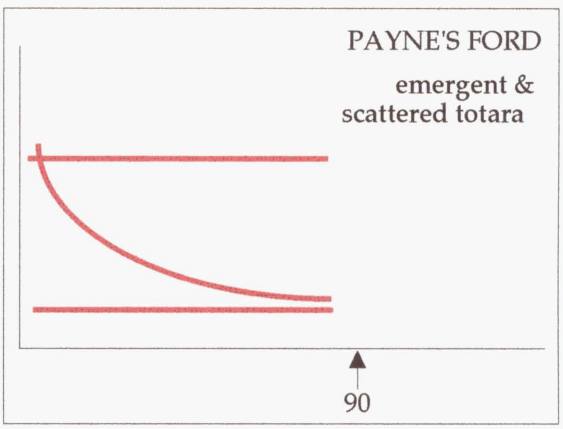
Figure 9.13 Stylized diagrams of stand growth through time (years B.P. versus mean ring width).

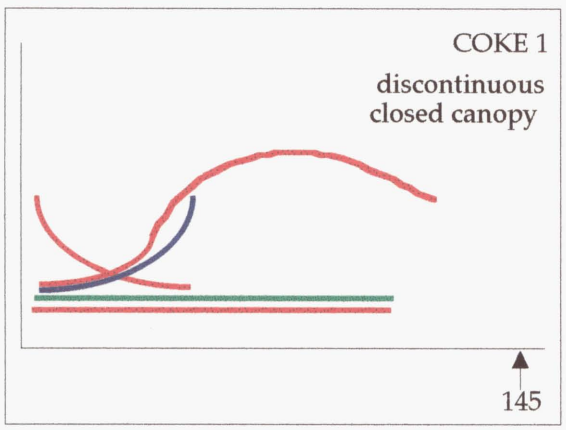
A. STANDS <160 YEARS OLD.

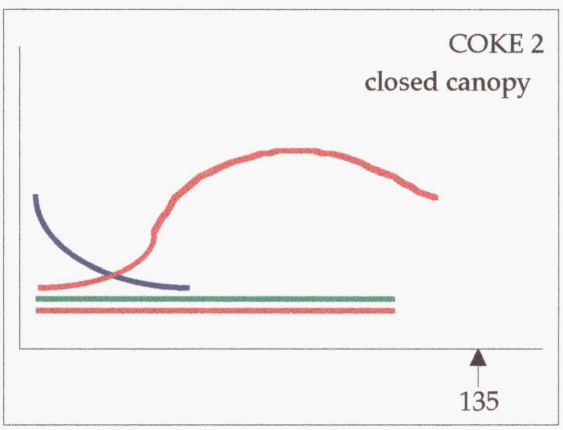


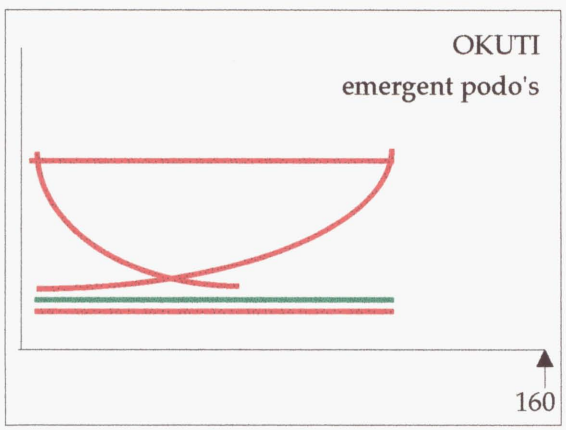












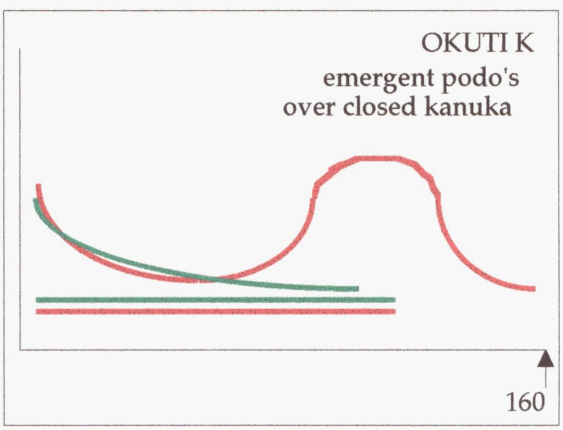
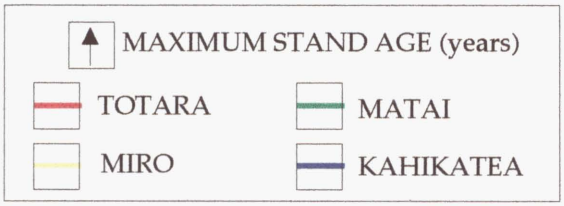
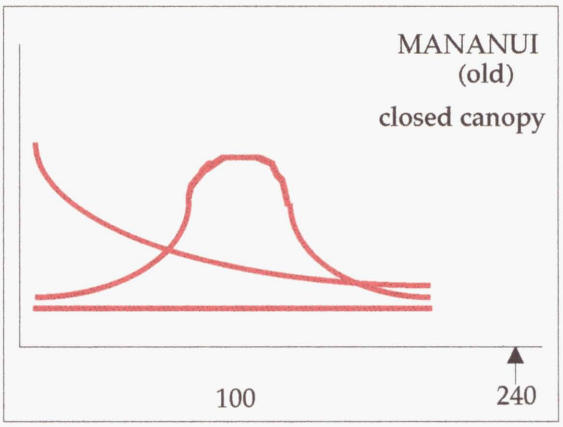
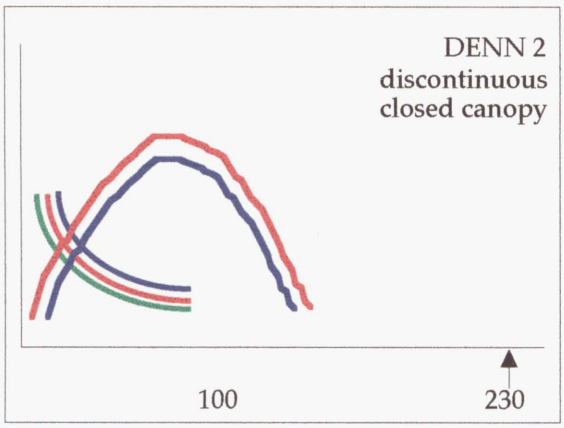


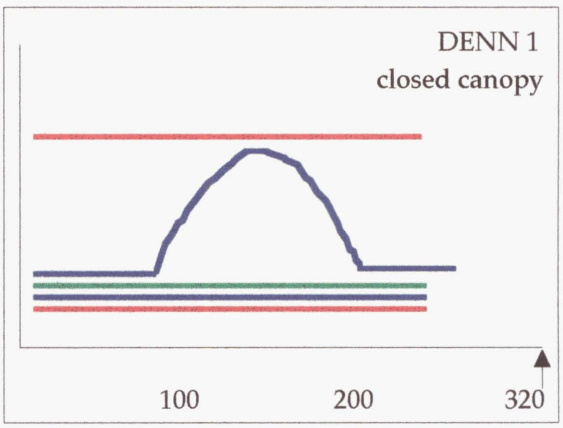
Figure 9.13 Stylized diagrams of stand growth through time (years B.P. versus mean ring width).

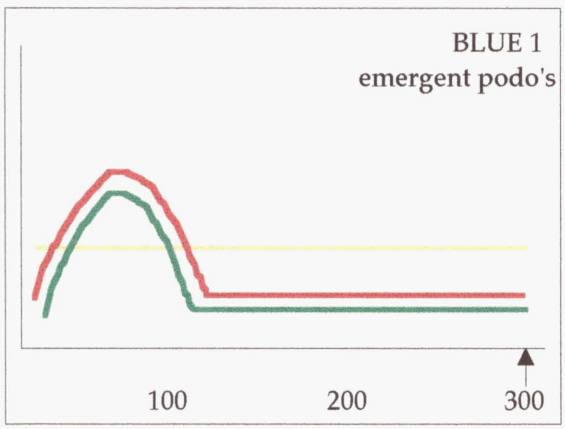
B. STANDS >170 YEARS OLD.

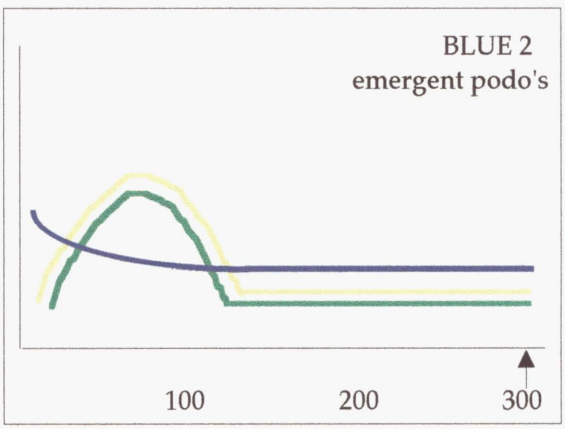












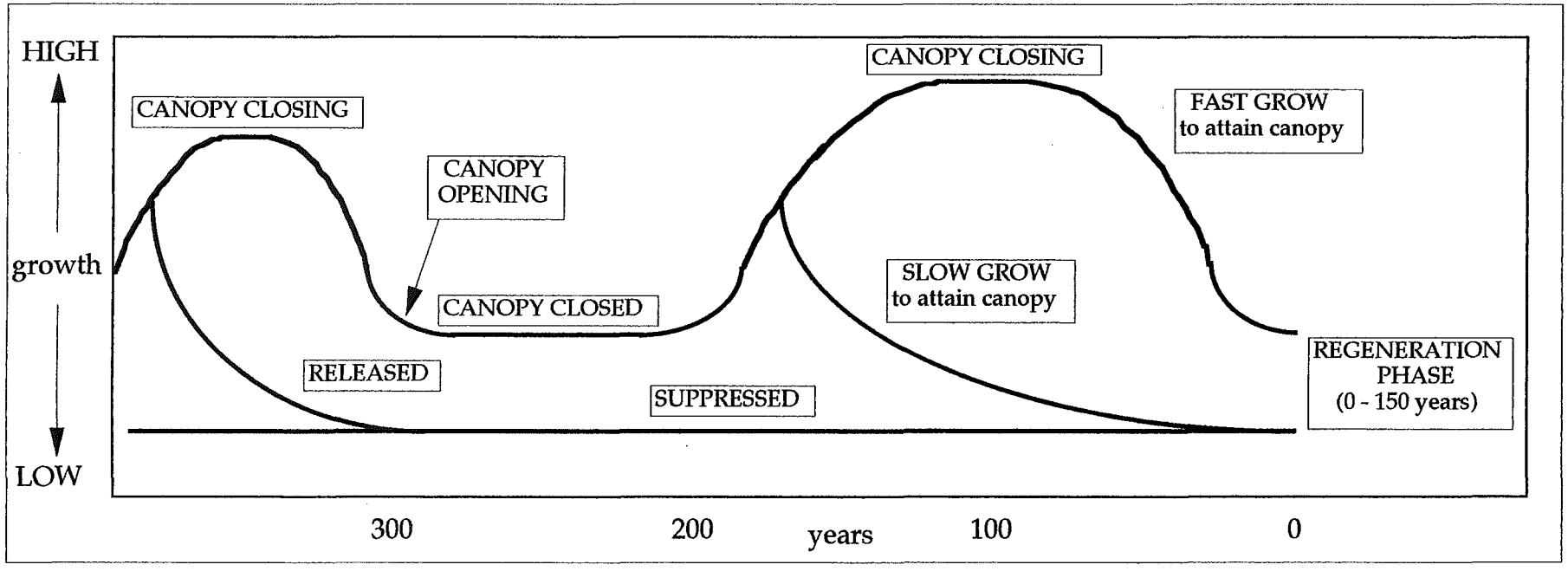


Figure 9.14 Generalised diagram of totara-dominated forest growth through time.

CHAPTER TEN
OVERVIEW OF ECOLOGY

10.1 THE ROLE OF DISTURBANCE IN PODOCARP REGENERATION

Detailed examination of stand age structure and spatial patterns can elucidate past and present regeneration. It is common to differentiate three main types of regeneration patterns in forest trees (Veblen 1982), based on the scale and severity of disturbance involved:

1. 'Catastrophic regeneration' refers to the establishment of most of a population during a short period in large openings created by infrequent massive disturbances such as fire, flood, mass movement, or large scale windthrow. This pattern is typical of shade-intolerant trees and will be reflected by large areas occupied by a group of similarly aged individuals i.e. even-aged.
2. 'Gap-phase regeneration' refers to regeneration in smaller canopy gaps, such as those resulting from the windthrow of one or a few trees. This response to more frequent disturbances will result in fewer age discontinuities and more of an all-aged structure.
3. 'Continuous regeneration' refers to the growth of shade-tolerant seedlings and saplings beneath canopies lacking obvious gaps, so that there is a continuous replacement of the older, dying trees. This would be expected to produce a continuous all-age structure even over small areas.

In the New Zealand context, a variety of regeneration requirements are seen among the podocarps. Miro can grow to maturity in small treefall gaps (Beveridge 1983, Smale & Kimberley 1986) although the total area required for persistence of a population through time has not been examined. Both kahikatea and rimu occasionally recruit into small openings although a more extensive removal of the overstory is required for cohort regeneration (Wardle 1974, Six Dijstra et al 1985, Duncan 1993). Westland totara (*Podocarpus totara* var. *waihoensis*) appears to require catastrophic disturbance to regenerate (McSweeney 1982). Other studies of kahikatea dominated forest indicate the catastrophic disturbance requirement for regeneration (Wardle 1974). Ogden (1985) sees the regeneration of New Zealand

conifers as resulting from both small and large-scale disturbance events, the interaction of the two often complicating interpretation of forest dynamics.

In New Zealand, two main age structures resulting from different scales of disturbance are often seen in podocarp forest; even-aged stands following catastrophic disturbance and all-age stands as a result of gap-phase or continuous regeneration. The first is an even-aged structure where the podocarps have regenerated following catastrophic disturbance with subsequent failure to regenerate beneath an established stand (Veblen & Stewart 1982). The presence of mosaics of relatively even-aged trees following catastrophic disturbance is well documented for other New Zealand canopy dominants: *Libocedrus* (Veblen & Stewart 1982, Stewart & Rose 1989), rimu (Herbert 1980, Katz 1980b, Six Dijstra et al 1986, Duncan 1993), kahikatea (Foweraker 1929, Wardle 1974, Duncan 1993), kauri (Ogden 1985), and dense mixed podocarps (Lusk & Ogden 1992).

The second main age structure documented is one of all-ages, suggesting establishment in treefall gaps (Duncan 1991), or during canopy collapse (Lusk & Ogden 1992). A wide age range has been recorded in central North Island podocarp forests for matai (Bellingham 1982, Lusk & Ogden 1992) and miro (Lusk & Ogden 1992), and in Westland for rimu (Six Dijstra et al 1986). Evidence exists of cyclic regeneration of successive podocarp cohorts occurring in either the absence of disturbance or following periodic disturbance in central North Island and Westland forests (Six Dijstra et al 1986, Norton et al 1988, Ogden & Stewart 1995).

Limited age data exist for lowland totara. While spatial autocorrelation in (Chapter 8) indicates that some stands show two or more patches of differently aged trees, all the stands aged except Mananui were considered to be even-aged and regenerated in one period following catastrophic disturbance. Mananui Bush appears to be constantly regenerating forward on the prograding dunes in response to new areas being made available for colonisation. In all cases matai has the most restricted age range and usually enters the stands just after totara and kahikatea have started to regenerate. Totara and kahikatea have a widespread age range although both can be considered to be even-aged because the range is approximately one tenth of the species' longevity (Ogden 1985).

The regeneration of the podocarps at different times during one regeneration phase appears to be a function of light levels. Large gap specialists need high light levels and have faster growth rates (Duncan 1991). Both totara and kahikatea require high light and exhibit greater growth rates (Ebbett & Ogden 1998) and so would

regenerate first following catastrophic disturbance which would destroy any previously existing canopy. In the present study, the majority of stands aged showed matai to have the most limited age range, entering the stands early although after totara and kahikatea start to regenerate and finishing its regeneration phase well before totara and kahikatea. Matai does not have the ability to respond to high light in the way that totara and kahikatea can (Ebbett & Ogden 1998). Other studies have shown a limited age range for matai, where it only regenerates during high light level periods (Lusk 1989, Lusk & Ogden 1992).

The canopy collapse theory proposed by Lusk (1989), and further discussed by Lusk & Ogden (1992) and Ogden (1995), states that species within dense podocarp forest will have a narrow age range if they only regenerate at the peak of canopy collapse of the previous cohort. Canopy collapse occurs when the dominant trees senesce, creating light gaps which allow miro to regenerate first (Ogden 1995). More shade-tolerant species can regenerate all the way through canopy collapse and subsequent closure, creating a wider age range.

However, totara and kahikatea respond well to high light and are not considered shade tolerant (Ebbett & Ogden 1998). They would not, therefore, be expected to regenerate for long periods of time under earlier individuals. There is no evidence to suggest that the stands studied in the present study are older than first generation and hence susceptible to canopy collapse. Totara dominated forest occurs on the most frequently disturbed geographical positions and it appears that stands rarely reach the age required for canopy collapse. The large tract at Dennistoun Bush is a mosaic of first generation stands which have been initiated by periodic large-scale disturbance events.

In the present study, likely disturbance regimes of each study site were identified. Regeneration was seen to occur in canopy gaps (Mananui), on flood surfaces (Dennistoun Bush, Coke Covenant, Price's Valley), following fire (Okuti Valley), and on prograding dunes (Nikau, Mananui). The active alluvial fan of Dennistoun Bush provides an insight into the effect of disturbance on forest composition. This area has received some attention and flood surfaces have been correlated to lowland totara dominated stand ages (Hall 1993).

Only Dennistoun Bush shows a correlation between earthquake events and stand initiation. Several of the other stands studied are inferred to be first generation following catastrophic disturbance which creates new colonisation surfaces: Nikau, Mananui (sea level change), Payne's Ford (landform change), Okuti Valley (fire),

Coke Covenant, Price's Valley, and Puhi Puhi (flood). Earthquake events may well have played a role in the initiation of these stands, i.e. earthquakes triggering landslips or river course changes.

Blue Duck is a more mature stand of dense podocarps and so it is difficult to determine whether it is first generation. However, evidence suggests this stand is first generation as a result of landslip as the podocarps are dense and totara occurs in distinct clumps within this forest type. A canopy collapse mechanism may be occurring at this site to maintain the dense podocarps in the absence of disturbance. Peraki Saddle is a relic population of totara/matai on the slopes of Banks Peninsula. As the other stands studied appear to be first generation, it is likely that this stand regenerated as a response to a landslip event.

Dennistoun Bush Huge is the only senescent stand in the present study. No evidence of regeneration under the opening canopy was observed. The occurrence of Dennistoun Bush Huge on an active alluvial fan with catastrophic flood deposition and earthquake events every 250 years seems to predispose this stand (and Denn 1 and 2) to periodic rejuvenation, resulting in a mosaic of even-aged first generation stands. Duncan (1993) suggests that in the absence of exogenous disturbance in the podocarp forests of Westland, angiosperms may well capture tree fall sites but will eventually be overgrown by the podocarps which are then re-initiated by catastrophic disturbance. Forest composition at Dennistoun Bush may not have time to change towards increased angiosperm abundance due to the almost clocklike regularity of large exogenous disturbance events which maintain a mosaic of dense podocarp stands.

Disturbance regimes favouring the regeneration of totara dominated stands appears to be in the medium to catastrophic range which initiate the development of an even-aged stand.

10.2 STAND ASSOCIATIONS AND NICHE PARTITIONING

Totara dominated forest forms a distinct forest type, occurring on catastrophically-disturbed, free-draining lowland sites. The occurrence of totara, matai, and kahikatea on fertile recent soils is well documented (Foweraker 1929, Beveridge 1983, McSweeney 1983, Hawkins & Sweet 1989b, Duncan 1991, 1993). In the present study, the most dense stands occurred on the most fertile soils, i.e. those found on alluvial plains and terraces subjected to periodic flooding disturbance. Stands

studied in this project, and where they predominate, range from pure totara to totara and all of the other podocarps. Distinct communities found were:

1. Totara/matai/kahikatea/rimu/miro
2. Totara/matai/kahikatea
3. Totara/matai
4. Totara

All of the sites except Mananui (where the high rainfall and free-draining sand promote leaching) have relatively high nutrient levels. Both totara and kahikatea respond well to high light and nutrient levels (Hawkins & Sweet 1989b, Ebbett & Ogden 1998, Ogden & Stewart 1995). The scale of disturbance may effect species composition. In a study on kahikatea floodplain forest, severe flooding was seen to remove all of the existing vegetation, leaving relatively homogeneous deposits of silt which was colonised predominantly by kahikatea (Duncan 1991). Mixed canopy stands with more rimu, miro, and kamahi are seen following less intense flooding which creates a variety of microsites (Duncan 1991). In the absence of siltation, a decline in nutrient levels may give rimu the competitive advantage (Hawkins & Sweet 1989b, Duncan 1991).

The totara/matai/kahikatea association only occurs at Dennistoun Bush where major periodic flood events deposit gravel and silt. Both totara and kahikatea show examples of a clumped distribution i.e. patches where each species is closely spaced. Gravel deposits which are free-draining appear to favour totara and silt deposits favour kahikatea (Foweraker 1929, McSweeney 1983, Wardle 1974, Ogden 1985, Wardle 1991, Ogden & Stewart 1995). Kahikatea and totara have a similar response to light of different levels and so appear to partition the environment on the basis of moisture or drainage.

The relative proportions of totara, matai, and kahikatea appear to be due to edaphic features such as fertility and drainage status. The proportion of kahikatea changes throughout the mosaic of Dennistoun Bush, indicating that either different amounts of silt and gravel were washed down in each major flood event or deposition was patchy. This edaphic/water content partitioning is also seen in river terraces in Westland (Foweraker 1929, Wardle 1974, McSweeney 1983).

Dense mixed podocarp stands occur on the less fertile soils such as those found in Mananui Bush and Nikau Reserve. The dense mixed podocarp association also occurs at Blue Duck Reserve, Kaikoura. Totara adults are more widely spaced here

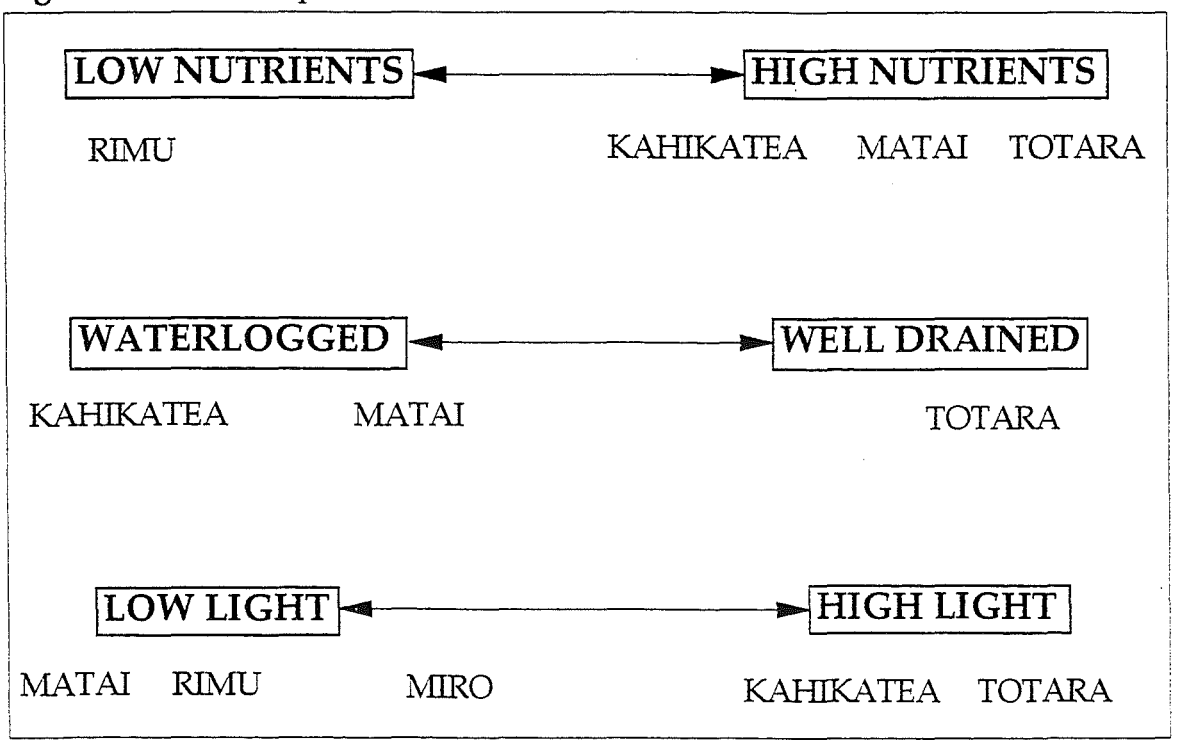
than in younger stands. In these less fertile sites, niche partitioning may occur, where each species is restricted to its optimal site in terms of drainage or light availability to obtain the competitive advantage.

Totara dominated stands require high light to initiate and capture a high fertility site, and relatively free-draining fertile soils to remain dominant. Sub-optimal totara sites will see the dominance of other species such as rimu. Totara will then be confined to its optimal niche, such as high fertility sites within the dense mixed podocarp forest which experience large scale disturbance.

10.3 GENERALISED MODEL

The podocarps have differing nutrient, light, and disturbance regime requirements and these factors work together to partition the environment into optimal areas for the regeneration and persistence of each species. Figure 10.1 shows the differing requirements of the podocarps which is based on results from the present study and previously published work.

Figure 10.1 Podocarp niches.



Totara, matai, and kahikatea occur on more fertile soils than rimu (Wardle 1991). Totara and matai prefer dry soils whereas kahikatea can tolerate water logged soils (Ogden 1985, Ogden & Stewart 1995). Totara and kahikatea dominate in

catastrophically disturbed areas, miro responds to medium levels of disturbance such as tree fall (Smale & Kimberley 1986), and rimu dominates in areas subject to continual disturbance such as canopy turnover (Six Dijstra et al 1985, Lusk & Ogden 1992).

Figure 10.2 outlines a general predictive model for the occurrence of different totara dominated forest types. In general, Hall's totara replaces lowland totara at altitudes above 450-500m, although Hall's totara can occur with lowland totara down to sea level if soils are relatively infertile.

10.4 SEEDLING ESTABLISHMENT

The importance of angiosperms in the distribution of podocarp seedlings is well documented. Bird species play an important role in the dispersal of podocarp seed - all of the podocarp species rely on bird dispersal for transport to suitable microsites and perch trees influence where seed is dispersed to (Beveridge 1973). Following catastrophic disturbance which removes the existing vegetation, the establishment of vegetation on these open sites may be a prerequisite to attract birds which disperse podocarp seed (Wardle 1974).

Podocarp seedlings in central North Island forests are often clumped under senescent kamahi due to the favourable light conditions under the canopy and the attractiveness of the perch tree to birds (Cameron 1955, Beveridge 1973b). This clumping of podocarp seedlings beneath kamahi is seen to reflect patterns of seed dispersal by birds (Beveridge 1964, 1973a, McEwen 1978, Norton 1991). Regeneration of podocarp seedlings has been observed away from parent trees but clumped beneath ageing broadleaf nurse trees (Beveridge 1973a, Herbert 1986, Lusk & Ogden 1992)

In the present study, examples of a clumped seedling distribution were observed both under angiosperms and parents. Spatial analysis results presented here for podocarp adults differ from that found for seedlings (see Table 7.5 and 7.6). Seedlings of all podocarp species show examples of being attracted to angiosperms whereas the adults all show examples of being repulsed from them. This indicates the temporal influence of angiosperm individuals within podocarp forest; seedlings are distributed around angiosperm perch trees whereas adults eventually capture the site, causing the angiosperms to regenerate between the dominant podocarps.

Seedling overhead cover and nearest neighbour results indicate the presence of different mechanisms for the establishment of the podocarp species. Seedling distribution analysis indicates that the three main canopy podocarps (totara, matai, kahikatea) have different regeneration strategies. Establishment of the seedlings and capture of a site may then based on edaphic and light conditions prevailing at each microsite which give each species the competitive advantage.

Totara can establish under both parent seed trees and bird perch trees although appears to prefer sites near parents, on dry (well-drained) level sites in the open (high light requirement). High light levels are required for seedling regeneration.

Kahikatea is repulsed from totara but preferentially distributed closer to angiosperms and appears to be confined in clumps on wet sites (poorly-drained). Kahikatea also has a high light requirement for regeneration (Ebbett & Ogden 1998, Ogden & Stewart 1995) and so niche partitioning with the similarly high light requiring totara occurs. This niche partitioning in terms of drainage is discussed by Ogden (1985). In Westland, kahikatea is seen to prefer wet depressions (Duncan 1991).

Matai is repulsed from totara adults and maintains a seedling population in mature stands due to its shade tolerance. This indicates matai's opportunistic or late successional strategy.

10.5 ADULT GROWTH PATTERNS

Figure's 8.1 and 8.2 can be used in conjunction with spacing statistics (Table 8.1), and spatial analysis (Tables 8.2 and 8.3) to elucidate the growth responses of the three main podocarp species through time. Totara shows significant correlations between size, age, and spacing, indicating the numerical and spatial dominance of this species. Totara individuals become more widely spaced with increasing size and age, possibly indicating a self-thinning mechanism. Spatial distribution of totara is either clumped or random, suggesting a preference for certain microsites, a clumped dispersal pattern, or patchy mortality.

Matai only increases its presence in terms of size rather than numbers or spacing whereas totara increases in both mean size and spacing with increasing age. Spatial distribution of matai is either random or uniform, suggesting that this species is late successional and can only capture those sites not already captured by the dominant totara. Spatial distribution of kahikatea is either clumped or random, also

suggesting a preference for certain microsites, a clumped dispersal pattern, or patchy mortality.

Ring width through time of two cores collected from randomly selected trees of totara, matai, and kahikatea show that trees exhibit constant variation in ring width around the bole, indicating that within-tree ring width variation is less than ring width variation through time. The use of the mean of two cores therefore accurately shows individual tree growth through time. No evidence of generic growth was encountered in the present study i.e. identifiable growth patterns can not be ascribed to specific diameter classes. Podocarp growth rates depend upon the light environment present rather than tree age or stage of development, i.e. high growth corresponds to high light levels. Bellingham (1982) also noted the lack of generic growth in matai.

Similar growth patterns through time are seen for all stands, regardless of forest type, presence of nurse crop, geographical position, or soil fertility. The regeneration phase lasts 50 - 200 years with totara and kahikatea regenerating first, followed by matai. Young stands show an initial period of high growth until the canopy closes. Suppressed individuals, predominantly matai, slowly grow to attain the canopy. Growth then slows with canopy closure (approximately 180 - 200 years after stand initiation) and maintains a low level of growth until release occurs. It would seem that this general pattern is repeated until catastrophic disturbance occurs to re-initiate the stand, either in the same location or nearby.

10.6 FUTURE STAND DEVELOPMENT

Generalised models of stand development and growth have been found for totara dominated stands (see Fig. 9.13) and can be used to extrapolate future stand development. Young/developing stands would be expected to continue their high growth rates until the dense podocarp canopy closes (180 - 200 years after stand initiation). Growth then slows to a steady low rate until individuals become emergent from the main canopy. Tree falls can also release individuals due to the increased availability of light.

Mature stands would be expected to maintain a steady low growth rate, associated with a continuous closed canopy, until individual tree falls occur to allow the remaining individuals to increase growth and take their place in the canopy (such as seen in Blue Duck). No seedlings or saplings were observed at Blue Duck and so the canopy openings, reflected by the released trees, may not have been large

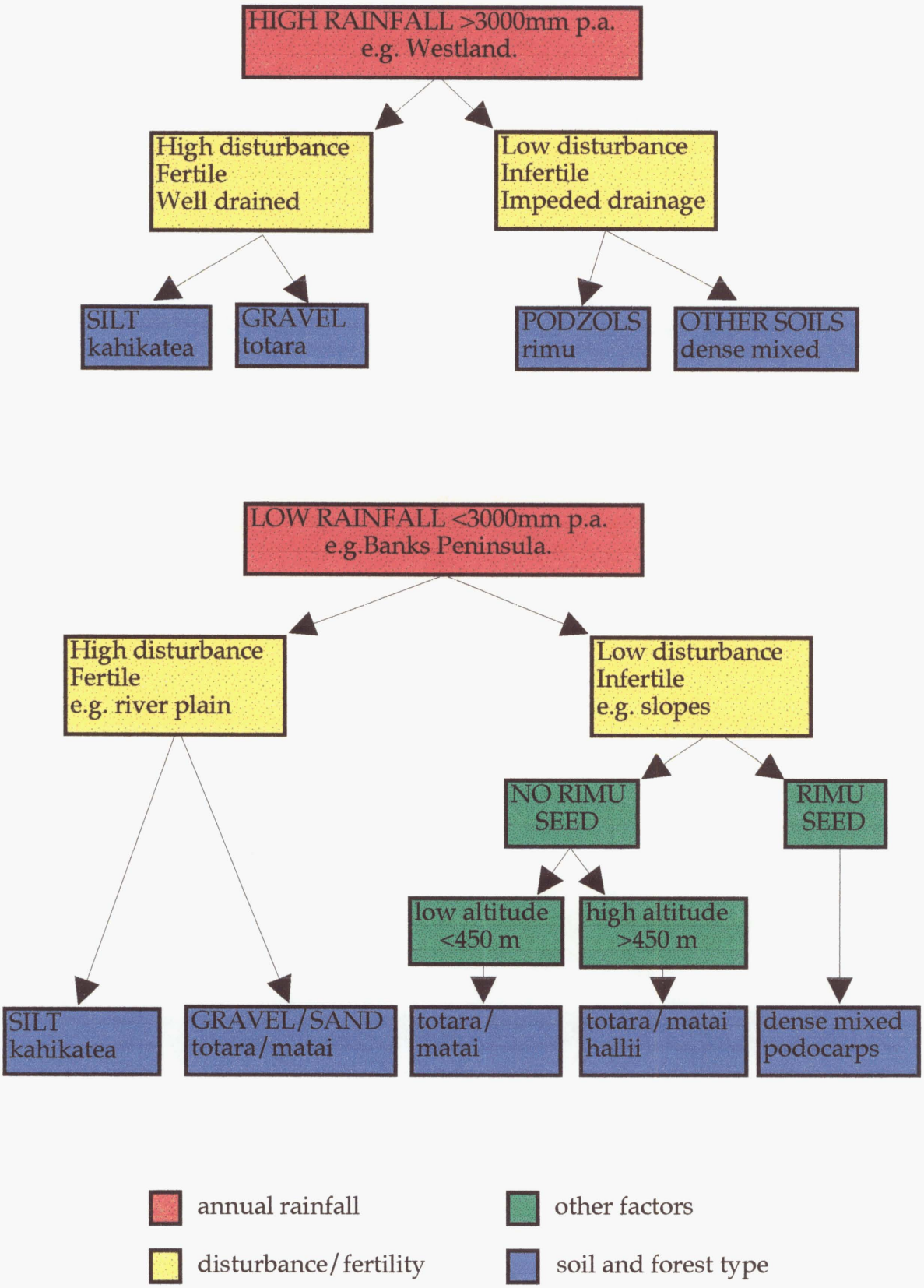
enough to allow the establishment of seedlings. In the absence of large-scale disturbance at Blue Duck, a canopy collapse process may well occur which allows for maintenance of the dense podocarp cover for several generations.

Unfortunately, almost all of the large totara in New Zealand have been felled for timber and so the study of senescent stands, and their replacement, is difficult. Podocarp seedlings (predominantly miro) have been observed growing under large totara (circa 1,000 years old) in Whirinaki State Forest Park, North Island but the majority of podocarp regeneration occurs under a nurse crop of *Weinmannia* which was burnt last century (Ebbett 1992). Senescent totara stands would be expected to have relatively high light levels, particularly upon the fall of a giant, high enough to allow the regeneration of some podocarps (particularly miro) until the next catastrophic disturbance event occurs to re-initiate cohort regeneration of the totara and kahikatea dominants.

The importance of catastrophic disturbance to the regeneration of lowland totara dominated forest is therefore clear. With the first aim of this study satisfied (to elucidate the ecology of lowland totara), the second aim now needs investigation (to assess the future survival of lowland totara in a fragmented landscape). Human activity may well alter the natural disturbance regime present at a site, hence the regenerative capacity of this forest type and future forest composition. Okuti Valley was the only study site to show regeneration as the result of humans, i.e. fire. This ability to regenerate following fire may appear auspicious for lowland totara but only if burnt areas are allowed to regenerate back to the original forest type.

The occurrence of lowland totara on areas desirable for pastoral activities (high fertility sites) means that interventionist management may therefore be required to ensure the future survival of this forest type, i.e. restoration and/or revegetation. Another important factor in the maintenance of lowland totara dominated forest are the effects of fragmentation on the distribution and future survival of this forest type. These issues are discussed in Part Three - Conservation of lowland totara in a fragmented landscape.

Figure 10.2 Generalised podocarp forest type predictive model.



PART THREE

CONSERVATION OF LOWLAND TOTARA IN A FRAGMENTED LANDSCAPE

INTRODUCTION TO FRAGMENTATION
INTEGRATED LANDSCAPE PLAN
CONCLUDING DISCUSSION

Plate 15 Brown granular loam hill soil on road cutting, Peraki Saddle, Banks Peninsula.

CHAPTER ELEVEN
INTRODUCTION TO FRAGMENTATION

11.1 INTRODUCTION AND OBJECTIVES

One of the most significant and widespread impacts of increasing human population and resource utilisation has been the clearing of native vegetation to create space for agriculture, forestry, and urban expansion. Deforestation has resulted in forest fragmentation, often with small isolated remnants remaining in a matrix of modified and highly disturbed non-forest habitat. The *Oxford Concise Dictionary* defines "fragment" as "a detached piece, an isolated or incomplete part, the remains of an otherwise lost or destroyed whole".

Different processes lead to forest fragmentation; (1) regressive fragmentation such as on the West Coast of New Zealand where forest clearing occurs from a single direction and the frontal edge is pushed back, (2) enveloping fragmentation when clearing and/or development pressures surround the perimeter of a tract, (3) divisive fragmentation when an intrusive force such as a road bisects a tract, (4) intrusive fragmentation when forest habitat is removed from within, and (5) encroaching fragmentation where a forest tract is removed from either side of a linear gallery forest, creating a corridor (Harris & Silva-Lopez 1992).

The overall trend of landscape modification is from predominantly spot disturbance patches due to resource utilisation, to introduced patches within large tracts, and finally to remnant patches or fragments which result from disturbance surrounding small areas. Examples of this process are clearly seen and documented for tropical forests (Bierregaard et at 1992), the Western Australian wheatbelt (Saunders et al 1987) and New Zealand (Ogle 1987). In fact, since the development of agriculture the native vegetative cover of every continent except Antarctica has been extensively modified (Saunders et al 1991).

Forest remnants have often been considered as habitat islands due to their small size and relative isolation. Insular habitats on the mainland have been discussed in terms of island biogeographical theory (MacArthur & Wilson 1967). In particular,

the importance of size, shape, species-area relationships, extinction and colonisation rates, and the design of nature reserves, have been much discussed in the literature (e.g. Diamond 1975, Simberloff & Abele 1976,1986).

The single large versus several small (SLOSS) debate has received particular attention (e.g. Higgs & Usher 1980). Simberloff (1988) has reviewed these areas of debate and so they will not be examined in any detail here. While of theoretical interest, most of these issues have no practical value in managing fragments or fragmented ecosystems (Zimmerman & Bierregaard 1986) although they do provide us with a conceptual framework for better understanding what might happen in small fragments.

In today's fragmented landscape, conservation managers and scientists must work with remaining remnants and practically never have the luxury of 'designing' reserves before an area is fragmented. Research and discussion should focus on the practical issues relating to the consequences of fragmentation on the biota, and the management of remnants for conservation.

The objectives of this chapter are to:
- Review and discuss the charactoristics and consequences of fragmentation for both plants and animals.
- Identify threats to remnants, management options, and research priorities.
- Identify consequences of fragmentation which are relevent to the future survival of lowland totara.
- Provide an example of fragmentation using Banks Peninsula as a case study.

11.2 CHARACTERISTICS OF FRAGMENTED ECOSYSTEMS

The biological and physical effects of fragmentation are poorly understood. Some changes are predictable, for example, population sizes will be reduced, habitat loss occurs, fragments become isolated, and the microclimate may change ie. physical fluxes (Bierregaard et al 1992). As few species are uniformly distributed within an ecosystem, any fragment of the larger tract will inevitably contain an incomplete sample of the larger block's indigenous species (Wilcove 1987).

Two primary effects of fragmentation, which leaves forest remnants within a non-forest matrix, are an alteration of the microclimate within and surrounding the remnant, and the isolation of each area from other remnant patches. Thus,

fragmented ecosystems are subject to both physical and biogeographical changes, the effects of which are modified by remnant size and shape (Saunders et al 1991).

11.2.1 Changes in microclimate

Radiation fluxes

Significant changes in the radiation balance occur from the replacement of perennial forest vegetation with pasture and crops - solar radiation reaching the ground is increased during the day, changing the albedo (Saunders et al 1991, Hobbs et al 1993a). Saunders et al (1991) state that in cleared areas, daytime temperatures are higher and night temperatures lower than in naturally vegetated areas. This leads to greater temperature ranges both at the surface and in the upper soil levels, increasing the incidence of frost.

The changes in radiation flux will have the most marked effect on the interface between the forest remnant and the agricultural/pastoral matrix, ie. the edge. In non-equatorial latitudes, the orientation of the edge has a significant effect on the degree to which radiation increases within a remnant at different times of the year (Ranney et al 1981) and the distance into the remnant where the radiation balance is altered. Air temperatures at the edge of a forest remnant can be significantly higher than those found within the interior. Kapos (1989) found that in tropical forest areas, temperatures were higher up to 40m into a remnant than the surrounding matrix and were also higher than the matrix in the core of a one hectare fragment. Young (1988) found significantly elevated air temperatures up to 100m into a remnant from the edge of New Zealand lowland broadleaf forest fragments. This phenomenon was also related to orientation, with elevated daytime and colder nightime temperatures penetrating further into north-facing edges.

The consequences of increased solar radiation at the edge are not clear. One would expect a different set of species to occupy this altered habitat, for example, colonising species which can utilise the increased temperature and light levels. Distinct sets of 'edge' and 'interior' species have been identified in fragments which have been isolated for a long time (e.g. Ranney et al 1981). Shade-tolerant species may become restricted to the interior of fragments due to competition from the edge species. Palik & Murphy (1990) found that the importance of sugar maple and beech increased from edge to interior, while that of less shade-tolerant species decreased. In their northern temperate study sites, the orientation of the edge also affected the species composition within.

While an edge may take some time to develop following fragmentation, the colonisation of the edge may effectively seal the remnant and maintain an interior environment similar to that which existed before fragmentation. The 'edge effect' has been reported for both tropical (Lovejoy et al 1986) and temperate systems (Ranney et al 1981). The edge zone and its protective buffering influence raises the question of remnant size and the maintenance of an interior environment, and will be discussed later.

Wind exposure

Saunders et al (1991) discuss the alteration in the pattern of momentum transfer due to the removal of the surrounding vegetation. Given the fetch requirements (i.e. minimum distance from vegetation boundary that will ensure that the wind profile has equilibrated) they suggest that a woodland with 20m high trees would need to be at least 2-4km wide before wind profiles would resemble those in an unfragmented forest system. This represents fragments in the order of 400 - 1600 hectares. Any smaller than this (and the majority are) would therefore exhibit an altered wind flow regime.

Fragments are obviously more exposed to wind, which may result in either physical damage to the vegetation or mortality due to increased evapotranspiration and desiccation (Lovejoy et al 1986). Trees near the exposed edges of recently isolated remnants are particularly at risk of windthrow because they have matured within a dense canopy and so do not have the structural qualities to deal with stronger winds than those to which they are accustomed. Windthrow creates canopy gaps, allowing particularly light-demanding species to recruit. Gap-phase regeneration is considered a major form of forest maintenance in many dominant canopy species both around the world and in New Zealand (e.g. Duncan & Stewart 1991, Ogden & Stewart 1995)

Increased exposure to wind at the interface between remnant and matrix has the secondary effect of increasing the transference of dust and seeds from the surrounding landscape (Saunders et al 1991). The arriving wind-blown seeds may be non-native weed species, hence altering species composition of the fragment, particularly at the edge. Saunders et al (1991) also suggest that the transfer of insects and disease organisms into remnant areas may be effected by elevated wind exposure. The effect of increased exposure to wind may once again be somewhat ameliorated by the formation of a secondary growth edge.

Water flux

Components of the hydrological cycle are altered due to the modification of the local water regime following fragmentation (Saunders et al 1991). Kapos (1989) suggests that the reason for decreased soil moisture near tropical forest reserve margins is due to direct surface drying and the higher evaporative demand of edge-positioned plants. She suggests that the magnitude of the decrease in soil water potential near the fragment margin could cause increased tree mortality due to water shortage.

Removal of the perennial vegetation (such as occurs in the agricultural/ pastoral matrix) reduces evapotranspiration due to the lesser root systems of crop species compared to forest trees (Saunders et al 1991) and hence alters soil water flows. Peak run-offs are increased as a result (Hobbs 1993) and topsoil is eroded and deposited downstream as sediment. Increased downstream flooding may be a result of deforestation (Hill 1985). An extra factor involved in the alteration of the hydrologic cycle is the rising of water tables and resultant salinity and waterlogging problems (Hobbs 1993).

The impact of water flux changes on a remnant depends on its position in the landscape. For example, remnants in mid-slopes and valley bottoms would be more affected than those at the top of a catchment. It follows that valley bottom fragments will experience soil deposition, which creates new substrates for plant colonisation, and higher erosion. Water running off pastoral and agricultural land would also be expected to contain abnormal levels (as compared to an intact forest) of animal wastes, byproducts, herbicides, pesticides, and fertiliser.

Saunders et al (1991) suggest that the management of the surrounding matrix will have impacts on the water flux of an area. For example, irrigation and drainage practices. They also identify further, but as yet undetermined, effects of changes in soil and surface moisture levels, e.g. changes in decomposition rates, altered seedbed characteristics, and changes in habitat for ground-dwelling fauna. Grazing stock will also introduce water flux problems in that they increase soil compaction and hence decrease water infiltration.

11.2.2 Isolation

Time since isolation

The importance of isolation in determining characteristics of biotic communities is one of the long-standing principles of island biogeography. Studies of islands formed by flooding suggest that an elevated species extinction rate occurs soon after the island is formed (Forman & Godron 1986). This elevated extinction rate is hypothesised to be rapid at first, then to gradually decline to zero as the island reaches a stable equilibrium number of species. The plant and animal species lost are often those with small population sizes or large territory requirements (Harris 1984). Harris (1984) states that upon isolation a forest remnant undergoes a 'relaxation period' (after Diamond 1975) as the fragment has more species than it is capable of maintaining.

A relaxation period appears to be just one portion of a longer modulation of adjustment which is characterised by an elevated rate of species dynamics. Following matrix disturbance and isolation of a forest fragment, some species will immigrate to the area and become established. This initial patch enrichment will then be followed by the more gradual species extinctions of the relaxation period. Forman & Godron (1986) suggest that this adjustment period of immigration and extinction may last for the life of the fragment i.e. until it converges with the matrix, although this may depend on fragment size.

If remnants are isolated for long periods of time, species extinctions are caused by diverse factors. The longer the fragment exists, the more chances there are of a species becoming locally extinct due to lack of recolonisation. Populations that are too small to be viable may persist for long periods simply because of the longevity of individuals. Hence, chronic remnant patches (i.e. those which remain isolated) have longer relaxation periods and more species are lost. If the remnant were to eventually converge with the matrix (i.e. matrix reverts to forest type present before fragmentation) it is likely to be very different from the initial vegetation.

The presence of a species in a fragment is no guarantee of its continued existence there; successful reproduction and recruitment are required (Saunders et al 1991). If the population is not viable in itself, seed dispersal from other areas is required. Isolation is therefore a function of the dispersal mode of species.

Long isolated remnants can be expected to have lost a certain amount of species and to have gained some species which are capable of establishing in a fragmented system (Saunders et al 1991). For example, light demanding colonising species which are able to successfully establish in remnant edges may go on to capture canopy gaps after windthrow events and hence invade the native vegetation and alter the species composition. These invasive weed/edge species can act to increase species number in a fragment (i.e. increase species diversity) although numbers of originally occurring species may continue to decline. Species composition must therefore be considered when managing fragments, rather than just species number.

Distance from other remnants

Isolation is largely determined by the ability of a species to colonise a remnant from other areas of native vegetation, rather than the distance *per se*. This colonising ability is related to dispersal mode e.g. wind-dispersed seeds are more likely to arrive at isolated remnants than those dispersed by mammals or birds (Saunders et al 1991). Animal species may be able to disperse seeds long distances but the matrix may act as an effective barrier to movement. Bierregaard et al (1992) found that a distance of 80m is a strong barrier to the movement of insects, mammals, and the vast majority of understorey birds in a fragmented tropical landscape. In the New Zealand context, the home range of the pigeon *Hemaphaga novaeseelandiae* may significantly affect the dispersal of native forest tree species such as miro, karaka, etc.

If any species have dispersal modes which do not allow for successful movement across distances of matrix or the nature of that matrix, the persistence of that species would then depend entirely upon its ability to maintain a viable population. Millar & Harris (1977) show that primate species loss is correlated with fragment insularity. As reserves are transformed from sample areas to insular islands (ie. effectively isolated) the increased insularity leads to isolation from surrounding gene pools. The resultant destabilisation of rare primate populations leads to conditions conducive to extirpation. Harris (1986) discusses the vulnerability of mammal species to extinction, citing small populations as a major cause. The concept of minimum viable population (MVP) is discussed further in a later section.

Quinn & Hastings (1987) suggest that fragmentation of a large population into isolated subpopulations may decrease the risk of overall species extinction even though local extinctions may occur. A population which is distributed in isolated

patches may be less susceptible to extinction from demographic stochastity or catastrophic events.

Connectivity

An associated effect of isolation is the degree of connectivity between adjacent areas. Saunders et al (1991) review the increasing attention to the issue of connectivity in the literature. The assessment of the value of corridors, movement of biota, and the management and rehabilitation of corridors is extensively discussed in Saunders & Hobbs (1991a), being the results of a recent workshop and conference on corridors. The benefits of corridors are considered to be enhanced biotic movement (and hence seed dispersal), the provision of refuges during disturbances, and enhancement of the aesthetic appeal of the landscape (Saunders et al 1991).

Studies on kangaroos (Arnold et al 1993) and white mice (Fahrig & Merriam 1985) show that populations in isolated woodlots are more prone to extinction than those in fragments with some degree of connectivity. The long-term survival of these species was questionable in the absence of corridors. Simberloff & Cox (1987) discuss potential disadvantages of corridors, including the facilitation of the spread of pests, diseases, and fire, increased predation, and high costs of maintaining linear remnants due to their high edge:interior ratio.

The value of corridors in a fragmented landscape will vary with target species. The movement of individuals across a landscape needs to be assessed in order to determine the merits and required characteristics of corridors (Saunders et al 1991). Obviously bird, mammalian, and invertebrate species have potentially the most to gain from the presence of habitat connecting corridors. Saunders & Hobbs (1991b) assert that in the absence of detailed information on the movement of biota across a landscape, a corridor network should be retained due to their potential benefits.

11.2.3 Modifying influences

Remnant size

The issue of island size has been extensively debated in the literature (Diamond 1978, Lovejoy & Oren 1981, Margules et al 1982). Theoretical and empirical evidence is available both for and against the assumptions generated by MacArthur & Wilson's (1967) equilibrium theory of island biogeography (e.g. Bierregaard et al

1992). This debate has now been somewhat superseded by the more important influence size has on fragmented ecosystem dynamics. Of particular importance is the edge-effect and the effect of size on how much interior forest remains in a remnant (Levenson 1981, Janzen 1983).

Pickett & Thompson (1978) suggest the concept of 'minimum dynamic area' as "the smallest area with a natural disturbance regime which maintains internal recolonization sources". While a valuable concept, the nature of old-growth forests are such that large areas would be required if all mosaic components are to be included, i.e. all stages of forest growth. Saunders et al (1991) suggest that a minimum dynamic area would only exist in the largest conservation parks.

An alternative concept for determining the minimum size for species persistence is MVP. Shaffer (1981, 1987) suggests that for long-term viability, populations need to be quite large (hundreds or more). Bierregaard et al (1990) state that an area of several hundred hectares is required for a MVP of a rare animal species in a tropical forest.

The larger a remnant, the more likely that a population will be able to resist chance extinctions (Nitecki 1984, Gilpin & Soule 1986, Soule 1987). The increase in habitat diversity in large remnants, as well a larger population size, contribute to a decrease in the risk of extinction (Diamond 1984). The actual number that constitutes a MVP will of course depend on the life history and population growth of the target species. While the issues of MVP have been extensively discussed in the literature, there is still no real resolution as to what constitutes a MVP. Problems of how to calculate MVP occur and in many cases data is not available. Most work done in this area concentrates only on vertebrates.

Larger populations have greater levels of heterozygosity. Saunders et al (1991) and Soule' (1989) state that current thinking is that heterozygosity is beneficial due to the retention of the genetic ability to adapt. The assumption that heterozygosity is essential for long-term population viability is, however, open to debate. Research is required on the demography of species and population size requirements for viability within a fragmented ecosystem. When considering forest tree species, an understanding of the dynamic requirements is also needed i.e. minimum dynamic area which will contain all developmental stages of the forest.

Several authors have investigated the edge:area ratio of fragments. From calculations of the edge-effect (which includes elevated solar radiation, exposure to

wind etc.), a remnant would have to be at least 2.25 hectares to have a one hectare interior core (assuming shape does not adversely effect the influence of external factors via the edge-effect). Calculations of edge-effect, and the minimum area required to have one hectare interior core is summarised in Table 11.1.

Table 11.1 Edge-effect and the minimum area required to have one hectare interior core.

Author	Edge-effect (m)	Disturbance Factor	Area for 1ha core
Lovejoy et al (1986)	25	solar	2.25
Kapos (1989)	40	solar/moisture	3.16
Harris (1896)	50	theoretical	4.00
Levenson (1981)	100	wind	9.00
Young (1988)	100	wind	9.00
Saunders (1991)	2000	wind	400.00

Saunders et al (1991) point out some of the disadvantages of large reserves; for example, the possibility of disease spreading through an entire population. The effect of reserve size on the biota is largely species dependent, highlighting the need for research on target species. Whether or not small fragments are viable entities or not is irrelevant when one considers the long-term goals of reintegration of remnants into the landscape and the establishment of network systems.

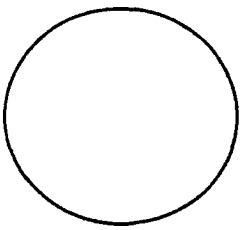
Remnant shape

The progressive modification of the landscape by both agriculture and urbanisation tends to eliminate narrow peninsula-like projections, straighten patch edges, and result in polygons, particularly rectangles. Diamond (1975) and Lovejoy et al (1984) state that the shape of remnants is only important for relatively small areas, where shape determines the edge:interior or perimeter:core ratio. Forman & Godron (1986) outline some of the important effects of shape on ecological processes (see Fig.11.1), all of which are strongly dependent upon the orientation of the long axis of the remnant.

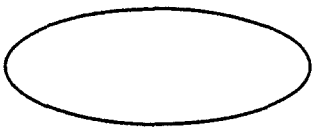
Once again, managers generally do not have the luxury of designing reserves and so the important question is how to manage reserves at present, no matter what shape, so as to minimise detrimental external effects.

Figure 11.1 Effects of shape on ecological processes (from Forman & Godron 1986).

Higher interior:edge ratio
Greater species diversity (with habitat diversity constant)
Less influence of edge effects on fragment total



Lower interior:edge ratio
Greater length of border and hence interactions with the matrix, greater susceptibility to invasion
Higher probability of barriers within a patch
Greater probability of habitat diversity within patch
Greater functioning as corridor for movement



11.3 CONSEQUENCES OF FRAGMENTATION

The primary impact of fragmentation is the loss of habitat. This reduction in size and extent has impacts on species diversity and population survival, as previously discussed. Community dynamics and landscape patterns are often determined by the prevalent disturbance regime, with fragmentation leading to an alteration of this regime, which may alter the long-term functioning and hence viability of communities (Hobbs 1987). Decreased size of a fragment increases vulnerability to external disturbances and reduces the area available for the natural (ie. prefragmentation) disturbance regime. Characteristics of fragmentation such as small size, isolation, and edge-effects also affect the stability and long-term viability of fragments, as previously discussed.

11.3.1 Alteration of disturbance regime

A disturbance regime is classed as the sum of types, frequencies, and intensities of disturbance through time in the landscape (Pickett & White 1985). Disturbance is considered as something that causes a community characteristic, such as species diversity, biomass, vertical and horizontal structure, to exceed or drop below its

homeostatic range of variation. The significant role of natural disturbance in the maintenance and coexistence of species through time is now generally accepted.

In order to persist within a particular disturbance regime, species must be able to complete their life cycles within this regimen. As disturbance frequency increases, some species are eliminated while other species, which can reproduce between or in spite of disturbance events, enter. These species are no longer competitively excluded by the original species. Where the disturbance regime has been elevated for some time, new ecotypes or even new species may evolve that are better adapted to the new disturbance regime (Reiners 1983). Genetic heterozygosity loss due to decreased population size and gene pool may affect the original species' ability to adapt.

Many natural events cause local or widespread disturbance e.g. fire, floods, storms, hurricanes, landslides, avalanches, earthquakes, volcanic eruptions, and extreme variations in climatic variables (Hobbs 1987). In addition to these relatively large scale disturbances are smaller scale events such as single tree falls. These smaller scale events are likely to occur more frequently. Aside from large scale disturbances, forest fragments are subject to internal and external disturbances. Fragmentation has many consequences, one of which is the alteration of the disturbance regime a forest is subject to. The importance of catastrophic and medium scale disturbance has been determined for totara dominated stands and so this modification of the disturbance regime is potentially critical for the future survival of this species.

External disturbances

Human-modified landscapes are changed by new disturbances introduced by people. Disturbances such as tree felling, air pollution, fire suppression, and the construction of roads and buildings are superimposed upon the natural disturbance regime (Forman & Godron 1983). The interaction between remnant areas and the surrounding matrix adds new types of disturbance to the existing regime.

One major externally originating disturbance with impacts on remnants is stock animals and the consequent grazing of seedling and soil compaction. It is clear that the successful conservation of a forest remnant depends upon the exclusion of stock. Other feral animals which can pose problems are foxes, rabbits, and wallabies, all of which can be controlled with 1080 or poison baiting (Hobbs & Saunders 1993). Atkinson (1989) discusses the effects of introduced animals on

indigenous terrestrial plants and animals. Specific effects of these aliens are predation, browsing, hybridisation, nest site competition, and the introduction of disease. The introduction of rats is of particular concern for seed predation and hence the potential to cause an alteration in tree population demography.

Small remnants are more exposed to wind which is likely to increase the occurrence of blowdown trees and canopy gaps. This wind induced mortality will be more obvious in the exposed edge, although small fragments will be exposed to an altered wind profile throughout. The importance of gap-phase regeneration in the maintenance of forest species has been well documented in the literature. Whether or not an elevated rate of canopy gap opening will aid the persistence of forest tree species will depend on the individual species' ability to capture gaps, which is in turn influenced by seeding periodicity, seed viability, microclimate preferences, shade tolerances, and competitive ability. Invasive weeds may require management if they detrimentally affect the native species through altering nutrient and water availabilities, and through impedance of the regeneration of native species.

The transfer of nutrients, pesticides, and organic matter (e.g. windblown stubble) are also external factors influencing a remnant. The method by which chemicals are applied to the land will effect how far they intrude upon a remnant eg. aerial spraying and upstream inputs are likely to cause higher levels of drift into a fragment.

Fire is another potential disturbance which may threaten remnants, particularly the spread of fire from burning crop stubble (Hobbs 1987) or for further land clearance. On the other hand, fire may be a component of the natural disturbance regime and so be beneficial, or even obligatory, in the regeneration and persistence of some species.

Lord & Norton (1990) state that the reduction in spatial continuity due to fragmentation, combined with edge-effects, increases the vulnerability of fragments to external disturbances such as windstorms and fires. The effect of extrinsic disturbances also varies with the nature of fragment dispersion ie. the scale of spatial fragmentation. Finer scales of fragmentation increase the vulnerability of vegetation to disturbance (Lord & Norton 1990). They suggest that at larger scales (ie. geographical fragmentation), the impact of externally arising disturbances can be minimised with the presence of appropriate buffer zones.

Internal processes

The importance of the internal disturbance regime for the long-term viability of fragments depends upon individual species' regeneration modes. What scale and frequency of what types of disturbance are required to maintain species and promote regeneration?

In the New Zealand context, a variety of requirements are seen among the podocarps. Miro can grow to maturity in small treefall gaps (Smale & Kimberley 1986) although the total area required for persistence of a population through time has not been examined. Both kahikatea and rimu occasionally recruit into small openings although a more extensive removal of the kahikatea overstory is required for cohort regeneration (e.g. Duncan 1991). Westland totara (*Podocarpus totara* var. *waihoensis*) appears to require catastrophic disturbance to regenerate (McSweeney 1982).

After fragmentation, remnant areas are likely to contain only a subset of the overall community states, i.e. stages in forest development. Loss of a state or species through disturbance of a community may not necessarily be matched by its reappearance elsewhere in the landscape (Hobbs 1987). There may not be sufficient area to contain all of the landscape mosaic units or forest development stages (i.e. non-equilibrium theory of patch dynamics) required for the long-term persistence of a species or community type. The small size of remnants, coupled with the successional stage requirements of forest tree species, means that some form of interventionist management may be essential to maintain a species within a fragment. Alternatively, adjacent areas could be included in the reserve system to allow for the shifting mosaic of regeneration stages, and hence ensure the long-term survival of species or type (Usher 1987).

Hobbs et al (1993b) suggest that fire is a major tool available to managers. Fire is recognised as a major type of disturbance required for the regeneration of many tree species and that plant diversity is increased post fire (Hobbs et al 1993b). Managers may need to consider the construction of fire breaks around remnants so that the internal fire regime is not significantly altered by wild fires of external origin.

Disturbance of various types is an integral part of community functioning. Fragmentation results in the decrease of recolonization sources with the consequence that extinction becomes the dominant population process. The internal

disturbance regime becomes critical for the maintenance of species (Pickett & Thompson 1978).

Management must be aimed at retaining the major aspects of the natural disturbance regime (i.e. those that are required for community self-maintenance), and at minimising the adverse effects of human-induced disturbances, or disturbances which are created as a result of fragmentation. In this respect it is vital to have knowledge of the prefragmentation disturbance regime in order to determine how it has been altered.

11.3.2 Threats to remnants

Perhaps the most significant and potentially destructive effect on forest fragments from the surrounding landscape is the invasion of the remnant by exotic species. Removal of vegetation from the surrounding area decreases the habitat remaining to the biota and leads to invasion of the fragment. Because fragmentation is usually due to human activities, remnant habitats are now generally in close proximity to areas of human disturbance. They may therefore be subject to excessive stress from internal invaders such as fire, pesticides, and weeds. In tropical regions the invasion of weeds from the surrounding disturbed landscape has two main effects, competition with tree species and enhanced ability of the dry weed biomass to carry fire (Carroll 1991). Saunders et al (1991) also report several papers which highlight these two effects; alteration of fuel structure and fire regime, and inhibition of native species regeneration.

Timmins & Williams (1987, 1991) discuss the characteristics of weed species which invade New Zealand natural areas. It was found that the most important characteristics influencing the number of problem weeds in reserves are proximity to towns, distance from roads and railway lines, human use, reserve shape, and habitat diversity. Reserves with the most weeds are narrow remnants on fertile soils with clearings. Carroll (1991) lists the main reasons why agricultural matrices can increase numbers of invasive weeds in a fragment as; agricultural land provides a greater source pool of invasive weed species due to the greater extent of disturbed land, propagules are transported readily due to tourism and commerce, and the edge:area ratio of fragments is large, enhancing the area available for invasion.

Non-native herbivores such as stock can also dramatically change the vegetation structure and prevent regeneration through increasing soil compaction. They also

remove the shrub and litter layers, exposing the soil to elevated temperatures. Plate 16 shows the eaten-out interior of Coke Covenant 2 where the remnant is not fenced off from cattle. This remnant also contains the invasive weeds holly, willow, and wandering jew. Loyn (1987) states that an intact understorey is important for predatory and parasitic insects as well as birds, which all reduce pest insects. It was noted that eucalypt dieback from defoliating insects was more severe in small, heavily grazed remnants. The effects of other invasive bird species are reviewed by Saunders et al (1991).

Plate 17 shows two totara forest remnants - Okuti Valley Scenic Reserve in an agricultural matrix of human disturbance, and Waikato Spit in Golden Bay currently being invaded by the dwellings of humans. The subdivision of forest remnants also poses a considerable threat to the integrity of the forest ecosystem remaining (Norton 1996).

11.4 FUTURE MANAGEMENT OF FRAGMENTS

11.4.1 Management options

The goal of conservation management is usually to maintain species diversity, which can be achieved by maintaining representative examples of each ecosystem, community type, or vegetation type (for example, the New Zealand Protected Natural Area survey technique, Kelly & Park 1986). In today's modified landscape, managers are usually required to deal with already fragmented systems and so must 'make the most of them'. The initial step is to understand the representative diversity of a region, which will then provide priorities for future acquisitions. High priority should be given to understanding the biology and ecology of species or vegetation types designated in being in special need of conservation due to their restricted distribution or rarity, either natural or fragmentation induced (Main 1987).

The fragmented reserve system must then be managed to maintain the diversity of the target species or ecosystems. The elements of change and heterogeneity need to be maintained because individual species require functioning ecosystems to survive. Walker (1989) suggests that we need to discard the notion of an idealised state for the ecosystem and allow change to occur. Ecological processes must be maintained in order to maintain ecological resilience, as well as providing the required dynamic regime for species persistence. Managers, through liaison with researchers, need to establish whether thresholds are likely to occur in ecosystem

changes and then intervene only when the threshold has been reached (Walker 1989). Interventionist policies may be required in the future to save rare species from extinction because the majority of reserves are too small to contain viable population or minimum dynamic areas (Soule' 1989). Problems that are likely to disrupt ecosystem processes and hence threaten the viability of a community or target species should be given high priority for treatment (Saunders et al 1991).

The management of fragmented ecosystems and the maintenance of diversity through maintaining ecological processes has two main components - management of the internal dynamics of fragments (e.g. vegetation dynamics, fire etc.), and the management of external influences impinging on the natural system (e.g. external disturbances such as grazing animals, weed invasion etc.) (Saunders et al 1991, Hobbs et al 1993b). Saunders et al (1991) state that for large remnants the emphasis should be on maintaining internal dynamics such as the natural disturbance regime and population dynamics of the key species because the relative influence of the matrix is decreased. Small remnants are more affected by the surrounding landscape and so management should be directed at external disturbances.

Traditional reserve management stops at the reserve boundary. From the current knowledge of landscape interaction we now see that a holistic strategy is required to ensure the long-term viability of our remaining natural areas, i.e. an integrated landscape management strategy. This landscape approach to management is the 'network' system advocated by several authors (Harris 1984, Forman & Godron 1986, Hobbs et al 1993b). Such a network would also contain linkages between other remnant areas, providing corridors for species movement across the landscape.

The added advantage of managing a network of fragments, remnant areas, and associated corridors, is the opportunity for landscape restoration and reintegration. Adjacent denuded tracts may not only provide areas for regeneration of catastrophic disturbance requiring forest species, but also have significant value in what they may become in the future.

11.4.2 Research priorities

The most important outputs of research on forest fragments or fragmented landscapes are those with direct relevance to management. Priorities must be clearly determined for both research and management, for example, what is our conservation aim? Sound management depends on a knowledge of the resources to

be managed and an understanding of the processes that sustain those resources. To this extent, research is essential to management (Hopkins & Saunders 1987).

Ridsdill-Smith (1987) outlines what types of organisms should be studied and monitored, and what methods could be employed i.e. autoecological versus community studies. The major priority areas for research have been identified by Soule' & Kohm (1989) and Saunders et al (1991):

•Research to date on fragmented ecosystems has provided few answers of practical importance. There is an urgent need for field experimentation with reference to management and restoration of fragmented ecosystems. Research has much to gain from a liaison with management, particularly if management operations can be carried out as designed experiments (e.g. the Habitat Island Project at Okarito, south Westland).

•There is an urgent need to understand the effects of external factors and to assess the consequences of these on fragments (Walker 1989). A parameter which requires evaluation is the abruptness of gradient between patches and the surrounding matrix, and between residual patches. Comparison between pre- and post-fragmented systems may elucidate more accurately the changes in water relations, radiation flux, and biotic invasions upon fragmentation. The relationship between external versus internal processes also requires further investigation.

•The question of heterozygosity and genetic change in isolated populations requires further study. Is the reduction in genetic variability important for the long-term viability of populations? What role do corridors play in the movement of species (and hence genes) through the landscape?

•Reserve planning requires detailed knowledge of the ecological and specific habitat requirements of target species (Bierregaard et al 1992). Perhaps an elucidation of minimum viable populations/minimum dynamic area for target species is required. Population viability analysis is an emerging branch of theoretical ecology. Soule' (1989) predicts that the accuracy of estimates of MVP's will improve in the next two decades, although a solid body of research is required for testing and refinement of the theory. Ehrlich & Murphy (1987) highlight some of the problems associated with studying populations in habitat remnants ie. bias due to microhabitat heterogeneity, and high edge to interior ratios. They suggest that studies on habitat remnants should be designed to enhance the understanding of

population processes leading to extinction, and those that aid in the management of reserves.

•The dynamic requirements of targets for conservation must be known. Once these are established, managers must ensure that the dynamic state is present and available to the entity of interest. The viability of many forest types depends upon the disturbance regime - what scales of disturbance are required?, does the fragment area and surrounding landscape provide adequate intensity of disturbance to ensure long-term viability?, to what extent are seed dispersers relied upon?.

A research approach is required that recognises how the regeneration and long-term maintenance of populations are tied to short-term fluctuations in the system dynamics (Harris & Silva-Lopez 1992). One must know the processes governing the system (both external and internal), the historic range of flux in the system, and the nature and impacts of episodic and long-term phenomena. A long-term perspective of the dynamics of a system will also aid managers in establishing policies with regard to changes in a system and their response (Walker 1989).

11.5 BANKS PENINSULA - A FRAGMENTED LANDSCAPE

11.5.1 The felling of the forests

With the cessation of volcanic activity, Banks Peninsula's fertile basaltic and loessic surface developed a continuous forest cover during interglacial periods, with the exception of very steep, exposed sites which were open tussockland. Podocarp forest was the predominant forest type, being most dense in alluvial valleys. Differing proportions of totara, matai, and kahikatea occurred in the lowland with Hall's totara becoming predominant on the upper slopes (Johnston 1961). A thin coastal association of ngaio, titoki, nikau, akeake, and broadleaf occurred while rimu and miro were very localised (QEII National Trust 1987, Wilson 1992).

The Banks Peninsula landscape has been dramatically modified in the last one hundred and fifty years, primarily through forest removal. The impact of Polynesian people was generally localised from land clearance for dwellings or cultivation and to facilitate travel. When the first Europeans settled on Banks Peninsula in the 1850's, two-thirds was still clad in forest but by the end of the century very little was left (Jonston 1961, 1969, Wilson 1992). Timber was required

for housing and public amenities at Lyttleton and Christchurch due to the arrival of the Canterbury Association settlers in the 1850's (Olgivie 1992).

Licences were granted from 1851 and the milling and export of timber began in earnest. In 1869 over 600,000 meters of timber was exported from Akaroa alone. Totara was considered by far the most versatile and valuable timber tree, being used for fence posts, bridging, telegraph poles, wharf piles, railway sleepers, and boat building. Matai, kahikatea, and miro, and rimu to a lesser extent, were also felled. Rimu and miro are now close to extinction on the Peninsula. Cut-over forest was then sold to farmers and fired for pastoral land (Olgivie 1992).

From the late 1850's onwards, Banks Peninsula was famous for dairy products and grass seed, mainly cocksfoot. Since 1950, sheep and beef cattle have formed the mainstay of the Banks Peninsula economy. Wool production occurs, as does deer farming and exotic plantations (Wilson 1992).

11.5.2 The present landscape

The Banks Peninsula District covers an area of 107,597 hectares. The topography is mainly disected and hilly, with sheltered valleys and exposed uplands. Summers are warm and winters are cool, frosts regularily occur as well as snow on the exposed ridgetops. There is a marked variation in climate on the Peninsula due to steep topography and the occurrence of microclimates. In the drier western region, rainfall is 400 - 700mm per annum (Banks Peninsula District Council 1997).

The Banks Peninsula landscape is now a mosaic of forest remnants, mostly occupying gullies where it has either survived fire or regenerated there because of the buffered environment. Old growth forest remnants are very small and occupy 800 hectares in all. Podocarp/hardwood forest represents a mere 0.7% of the Banks Peninsula land area. There is around 6000 hectares of second growth hardwood forest, of which circa 3000 hectares is predominantly kanuka (Wilson 1992).

Around 74,000 hectares is pasture, tussockland, open shrubland, fernland, sedgeland, and rushland - approximately 74% of the Peninsula's surface. More than 16,000 ha of this has reverted over the decades to native bracken, shield fern, rushes, or shrubs like *Coprosma*, or else to exotic gorse or broom (Wilson 1992). The use of gorse in the revegetation of areas is now widely accepted as long as it does not burn until native seedlings have overtopped the gorse canopy (e.g. Wilson 1994).

Remnant distribution

The distribution of all significant forest remnants on Banks Peninsula (reserved or recommended for protection) containing scattered lowland totara or areas of lowland totara forest (n=72) is shown in Figure 11.2. Almost all occur below 500m altitude, which is the zonal limit where lowland totara is replaced by Hall's totara or hybrids between the two species in the lower montane region (Hugh Wilson pers.comm.). Remnants are larger and more prevalent on the south-western side of the Peninsula and very small and widely spaced on the north-eastern side. This may reflect settlement patterns based on prevailing wind patterns.

Preest (1963) states that podocarp regeneration presumed to be the result of bird dispersal can be seen many kilometers from the source, frequently associated with suitable perching places. McEwen (1978) discusses the habits of the new Zealand wood pigeon (*Hemiphaga novaseelandiae novaeseelandiae*). Birds are known to move from place to place follwoing the supply of fruit. They also migrate seasonally to escape harsh winter conditions or to find fruit. In the only study located on bird dispersal distances, Burke (1974) found lowland totara seed had been dispersed 4.8km.

Mean distance to nearest neighbouring lowland totara-containing remnant is 1.99km ± 0.87 s.d., measured off Figure 11.2. This seems small enough for the cross-remnant visiting by bird dispersers, although many remnants are separated by ridges. Most remnants are surrounded by a predominantly pastoral matrix (pers.obs.). The nature of the matrix may also affect bird movements.

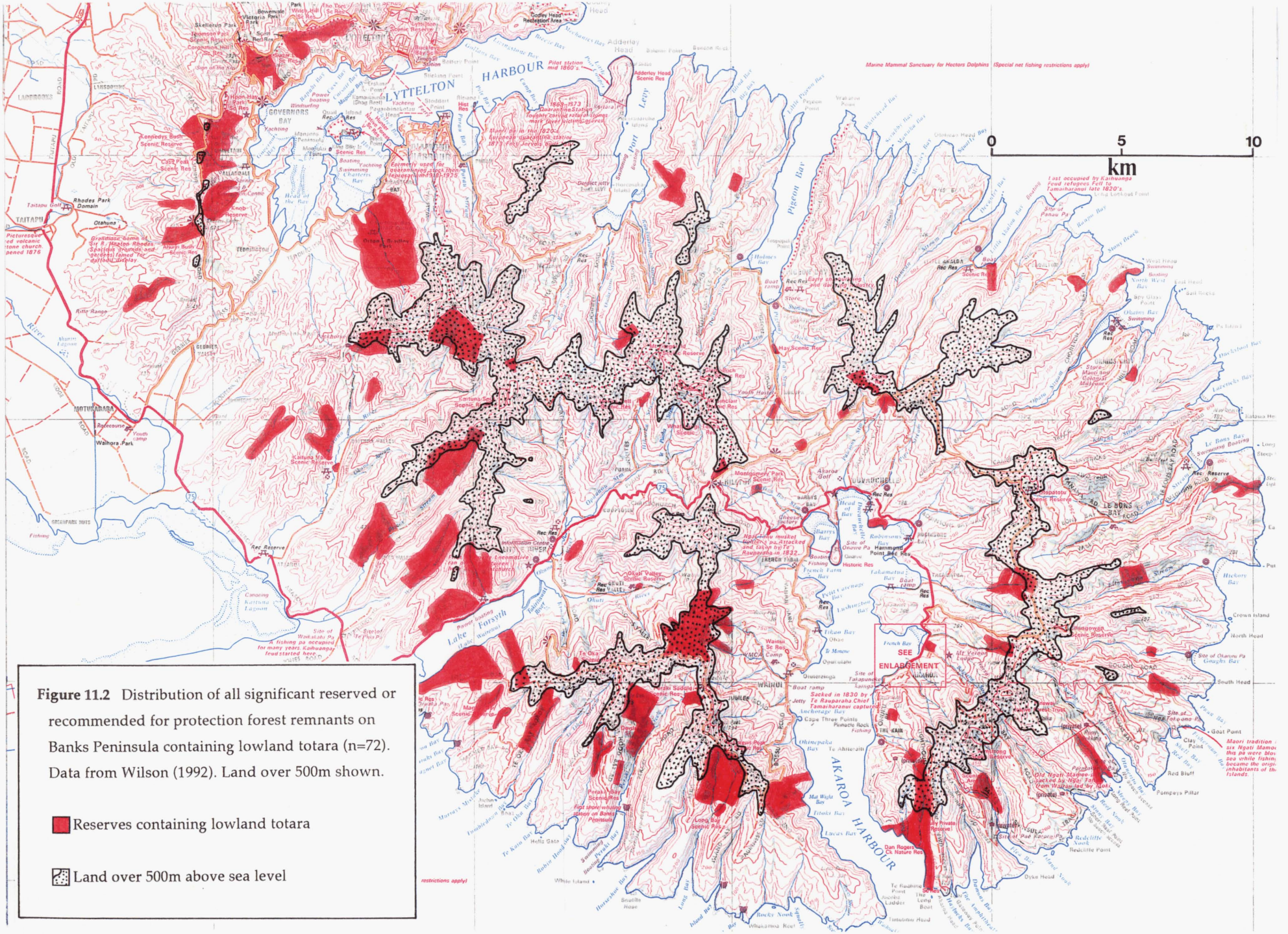


Figure 11.2 Distribution of all significant reserved or recommended for protection forest remnants on Banks Peninsula containing lowland totara (n=72). Data from Wilson (1992). Land over 500m shown.

Remnant size

Figure 11.3 shows the size distribution of all Protected Natural Areas and Recommended Areas for Protection containing lowland totara in Banks Peninsula Ecological Area (data from Wilson 1992). Protected Natural Areas are mostly under 10 ha whereas Recommended Areas for Protection are much larger. Figure 11.4 shows the size distribution of the lowland totara forest component within all significant remaining remnants on Banks Peninsula (data from Wilson 1992).

Figure 11.3 Size distribution of all Protected Natural Areas (PNA) and Recommended Areas for Protection (RAP) containing lowland totara, n=72 (data from Wilson 1992).

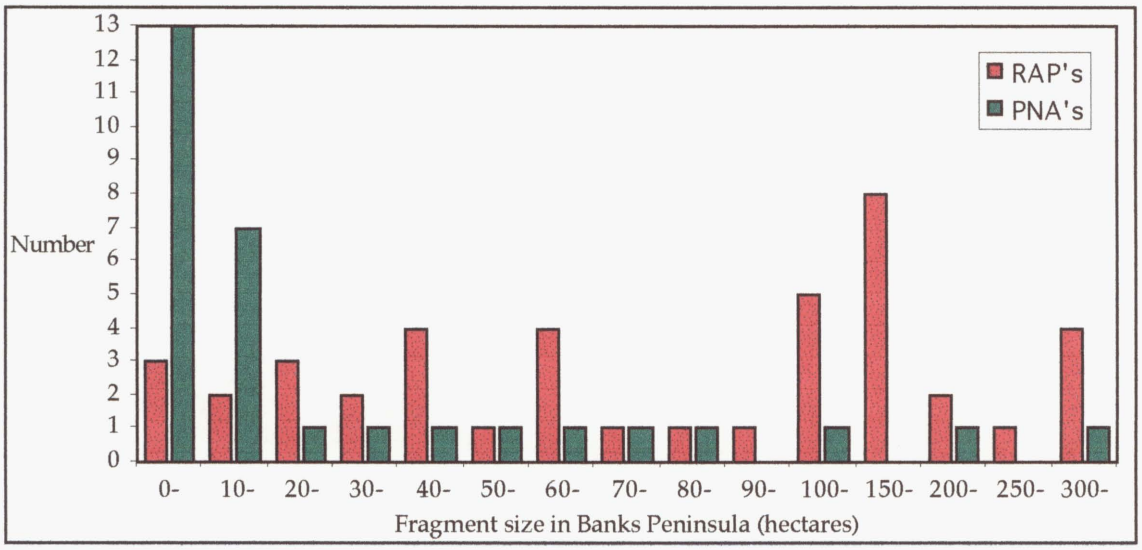
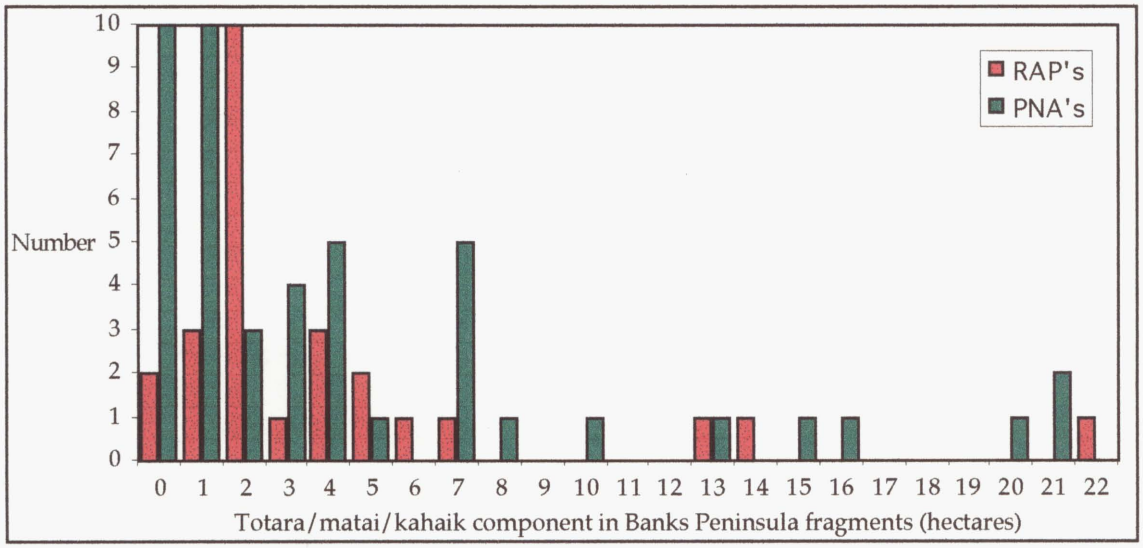


Figure 11.4 Size distribution of the lowland totara forest component within all significant remaining remnants on Banks Peninsula, n=72 (data from Wilson 1992).



Mean size of the lowland totara forest component in all significant remaining fragments containing lowland totara is 4.7 ± 5.6 hectares (data from Wilson 1992, n=72). Based on number of lowland totara trees per hectare obtained in the present study this size of fragment would contain a lowland totara population of 61 senescent individuals, 400 individuals on the less fertile colluvial slopes, and 1457 individuals on fertile alluvial terraces and river plains which represents the most dense stand observed.

Remnant shape and position

Table 11.2 outlines remnant shape and topographical position for all significant fragments containing lowland totara dominated forest. Remnant shape varies from predominantly square and rectangular to more irregularly shaped. Remnant boundaries are mapped in Wilson (1992) and assigned either square/rectangular, round, or irregularly shaped depending upon which shape they most resemble.

Round shaped remnants, which have the greatest interior to edge ratio, are the least prevalent shape. Fifty percent of remnants are in colluvial slope positions where less dense lowland totara forest dominated stands occur. Valley remnants represent 37.5% of the fragments. Very few coastal forest remnants are represented in the current Banks Peninsula reserve system.

Table 11.2 Remnant shape and topographical position of all significant remnants containing lowland totara dominated forest on Banks Peninsula (n=72).

SHAPE	n	%	POSITION	n	%
Rectangular/square	39	54	Colluvial slope	36	50
Irregular	21	29	Alluvial valley	27	37.5
Round	12	17	Coastal	9	12.5

11.5.3 Managing the landscape

In terms of managing the fragmented Banks Peninsula environment, and improving it in the future, incentives for landscape protection include the following (QEII National Trust 1987):

•Queen Elizabeth II National Trust Open Space Covenants - An agreement is reached between a private landowner (or leaseholder) and the QE11 trust in perpetuity whereby the owner volunteers to manage the land in a way that is

detailed on the covenant. This binds the present and subsequent owners as the covenant is registered on the land title.

•District and Regional Schemes - The district schemes of Akaroa, Wairewa, and Mount Herbert Counties as well as the Canterbury United Council's regional Planning Scheme include in their general aims provision for the protection and enhancement of the special qualities of the district's landscape. Local authorities may also be willing to negotiate rate relief for protected areas.

•Historical Places Trust - The Historic places Act 1980 provides legal protection to all archaeological sites. Any site associated with human activity more than 100 years ago is covered and owners should consult the Historic Places Trust before disturbing, modifying, or removing the site.

•Wildlife Refuge - Wildlife and habitats can be protected under the Wildlife Act 1953. Owners can contact the Department of Conservation to arrange for classification of areas as a wildlife refuge. This status can be revoked by either the owner or the Department of Conservation.

•Department of Conservation - Under the Reserves Act 1977 the Department of Conservation can protect land of important recreational, natural, or other special value by either purchasing reserves or declaring the area "protected private land" or making an area subject to a conservation covenant. The two latter methods allow the landowner to retain land ownership.

•Advice - Landscape planning and design advice can be sought from private landscape consultants as well as landscape planners working in Government Departments such as the Department of Conservation and Department of Soil and Land Information.

The management of a fragmented landscape is discussed further in the next chapter which uses a catchment in Banks Peninsula as a case study. Public opinions are used to determine which management options may be most appropriate for the area. The future survival of lowland totara forest is also discussed in terms of disturbance regime, reserve distribution, and past and present land use. An integrated land management plan is presented which provides for both productive and sustainable land use, and the future survival of lowland totara dominated forest within the existing rural pastoral matrix.

Plate 16 Stock damage to understorey, Coke Covenant 1, Collingwood, Golden Bay.

Plate 17 Threats to remnants; (A) Human settlement, Waikato Spit, Golden Bay, (B) Forest remnant in agricultural matrix, Okuti Valley Scenic Reserve, Banks Peninsula.

A

B

CHAPTER TWELVE
INTEGRATED LANDSCAPE PLAN

12.1 INTRODUCTION AND OBJECTIVES

Nature conservation problems cannot be isolated from the problems of land degradation in the agricultural matrix in which forest remnants survive (Hobbs & Saunders 1991). Recent studies suggest that management of a fragmented population should proceed via investigation of the ecology of the species in question (Hopkins & Saunders 1987) and the use of integrated landscape management, particularly in production environments where it is desirable to preserve both public and private utility of the land (Hobbs et al 1993). Integrated landscape management takes into account social, economic, and ecological factors. Ecological factors include soil type, topography, vegetational composition, disturbance regime, erosion processes, and waterway patterns. Social factors include landowner attitudes, financial considerations, and existing land use.

This chapter provides a case study for the design of an integrated landscape management plan on a catchment level to provide for the future survival of lowland totara in a fragmented environment. Integrated landscape management takes into account social, economic, and ecological factors. Ecological factors include soil type, topography, vegetational composition, disturbance regime, erosion processes, and waterway patterns. Social factors include landowner attitudes, financial considerations, and existing land use. Integrated land management and its benefits are discussed by Kubricki et al (1993) and Bradby (1991).

The entire Okuti Valley catchment, Banks Peninsula, is used as the study area. Past and present land use is determined, as well as public attitude to trees in the landscape and integrated land management. Due to the nature of the topic, the future of lowland totara is not discussed in isolation. Natural systems are never homogeneous but are mosaics of patches at any scale of resolution (Pickett & White 1985). Lowland totara dominated remnants occur within the existing heterogenous

landscape framework and so must be included in a general landscape plan with the aim of both forest protection and enhancement and sustainable land use.

Agroforestry is introduced as an alternative, sustainable, land management system - animals, crops, and woody perennials are grown together with the objective of stabilising and increasing overall land productivity. The benefits of multiple use systems include:

- Social aspects - the creation of a new resource and new employment
- Economic benefits - land gives a higher and more stable return
- Ecological advantages - soil and water conservation, improving of soil structure, improved pollination, richer habitat increases wildlife, stock shelter, new microclimates created.

The New Zealand Government has recently released the Sustainable Land Management Strategy (Ministry for Environment 1996). The desired outcomes for sustainable land management are:

- Maintenance of the potential of New Zealand soils for a range of uses for present and future generations
- The adoption of land management skills and the application of appropriate technology to enable individuals and communities to provide for their social and economic well-being
- The adoption of management practices that maintain or enhance the quality of groundwater resources, coastal waters and waterways
- The avoidance, and mitigation of the impacts of land-related hazards, including erosion
- The maintenance of aesthetic, ecological, cultural, and conservation values related to land and water.

While sustainability is a recent goal in New Zealand land management, few studies address the problems associated with fragmented native species (c.f. Widyatmoko & Norton 1997) and the applicability of integrated land management in solving these problems.

The objectives of this chapter are:

- To provide a case study of one representative catchment on Banks Peninsula. To address this objective, the following research questions are posed:

- what land owners think about integrated landscape management and trees in the landscape.

- what is the past and present vegetation pattern of the study area and how has it changed?
- what are the landscape parameters of the study area?

• To determine the suitability of integrated landscape management at the catchment level for improving the biological conservation of lowland totara while allowing for other land uses.

12.2 OKUTI VALLEY STUDY AREA

Okuti Valley is located in Banks Peninsula District, on the south-west part of Banks Peninsula and was chosen for both logistical reasons (within close proximity to University of Canterbury, small enough to work with readily) and ecological reasons (Banks Peninsula was a former stronghold of lowland totara in pre-human times, the catchment is well defined, and diverse land use already occurs in the community).

Less than one hundred people live in Okuti Valley at present. Primary land use remains livestock farming, both sheep and cattle. Dairy farming is in decline. Recent developments in Okuti Valley include deer farming, agroforestry, tourist attractions, and diversification into fruit and vegetables on the better quality soils (Wairewa County Council no date). Land use (past and present) is discussed further in section 12.4.3.

The main vegetation of the catchment is pastoral grasses with tussock occurring on the higher altitude ridges. Areas of kanuka and broadleaves occur in gullies, as well as scattered gorse, broom, and bracken. Two reserves are present, Okuti Valley Scenic Reserve of 4.3 hectares on the river terrace consisting of totara/matai/kanuka forest, and Te Oka Scenic Reserve of 11.6 hectares in the lower montane zone consisting of secondary kanuka/broadleaves with some remnant podocarps. Some recent plantations have been undertaken (Plate 18B).

12.3 METHODS

12.3.1 Questionnaire methods

Before any landscape management plans can be implemented it is important to understand the social environment in which it will work. Scientists can not expect to work in isolation and then tell people what to do with their land. For this reason I thought it important to canvas public opinion on attitudes to trees in the

landscape and other land management issues before proceeding with a theoretical integrated landscape plan.

A questionnaire was written, checked by a social scientist (Dr Alison Loveridge), approved by the University of Canterbury's Human Ethics Committee, and delivered to 125 households in the Okuti Valley and Little River areas. This represented practically every house in the area. 1981 census figures give the population of Okuti Valley and Little River areas to be 339 and so the questionnaire represents a sample of 37% of the total population.

Only one response per household was asked for, due to sampling biases which may occur in the same household. To protect against answering bias, questions were made as specific as possible with little room for personal interpretation. Inferences need to be made on the necessarily incomplete information from the sample group. Most statistical theory is directly related to or in support of making generalisations or inferences about populations from samples (Lapin 1975). As I had no control over who in the household responded, responses are assumed to represent a random sample to which statistical theory can be applied.

Full details of correspondence and the questionnaire appear in Appendix Four. Respondents were given three months to reply in a post-paid return envelope. Data was then collated and appears below. The final response rate was 51.2% (64 people), which represents 19% of the total population of the area and half of the households in the area.

Questionnaire respondents where asked about their attitudes to native and exotic trees, provision for land management, and any problems encountered with neighbours. These questioned were designed to glean information on public attitudes to trees in the landscape and land management, as well as identify areas where integrated land management may be of advantage. Current and potential land use issues were also canvassed.

12.3.2 Forest extent change

Forest extent and changes in land use through time were determined by comparing aerial photographs from 1945 and 1985 (supplied by New Zealand Aerial Mapping) with ground-based observation in 1995 to confirm vegetation types. Forest extent change therefore represents a 50 year period (1945 - 1995). For measurement purposes, vegetation was classified into four categories: native forest

(podocarp/broadleaf), scrub (bracken/gorse /kanuka/broadleaf), exotic forestry plantations, and exotic plantings such as gardens and windbreaks. Many authors have used multi-temporal panchromatic aerial photographs to classify and map vegetation although little attention has been paid to natural habitats (Green et al 1993).

Vegetation types were delineated on the aerial photographs after confirmation from ground observation and the amount of each type recorded using grid measurement (1 hectare grid used). Hectare values given are only approximate as aerial photographs are two dimensional and accurate values, taking slope into account, were not determined. Vegetation type changes were then expressed as percent change through time.

12.3.3 Okuti Valley landscape parameters

In order to produce an integrated landscape management plan, ecological parameters of the catchment such as soil type, potential land use, and erosion potential, needed to be determined. Catchment boundaries were defined on a topographical base map with land owner boundaries overlayed (data from Wairewa County Council no date). Soil types, slope, and erosion potential were identified using New Zealand Land Resource Inventory maps (MW&D 1975, Van Berkel 1984).

12.3.4 Integrated landscape plan

In order to develop an integrated landscape plan which takes into account the ecology of lowland totara, various scales are identified to be of importance. The distribution of lowland totara on the National Scale (see Chapter Four) describes the broad scale pattern, i.e. lowland totara is confined to land under 500m above sea level, mainly on alluvial terraces and river plains. The Regional Scale of distribution is then superimposed, with climate and geology being the major determinants of lowland totara distribution. Regional distribution is also important for the survival of lowland totara in terms of dispersal distance and forest associations present in a region.

The present plan is at the catchment scale and is dependent upon the current vegetation pattern and landscape parameters. The fine scale of the plan is then determined by landowner attitudes, and property boundaries. The current extent of forest and current land use in the catchment will be used as a basis for the

integrated landscape management plan. Native forest and scrub remnants provide nuclei for forest regeneration throughout the catchment. Exotic forest plantations are based on both existing use and potential areas for development. Plantation and shelterbelt distribution is based on the design guidelines of the Banks Peninsula District Council's proposed district plan (1997) and Lucas (1987).

12.4 RESULTS

12.4.1 Okuti Valley study area

Okuti Valley study area results appear in Figure 12.1. The majority of residents have lived in the area for less than five years although many are long-term residents (>20 years in the area). Main reasons for living in the area are that its a nice place to live, has a good community (village), is close to Christchurch for commuting purposes, and has a good climate. Nearly half of the respondents are involved with sporting activities, although volunteer work, school committees, and social clubs are also popular.

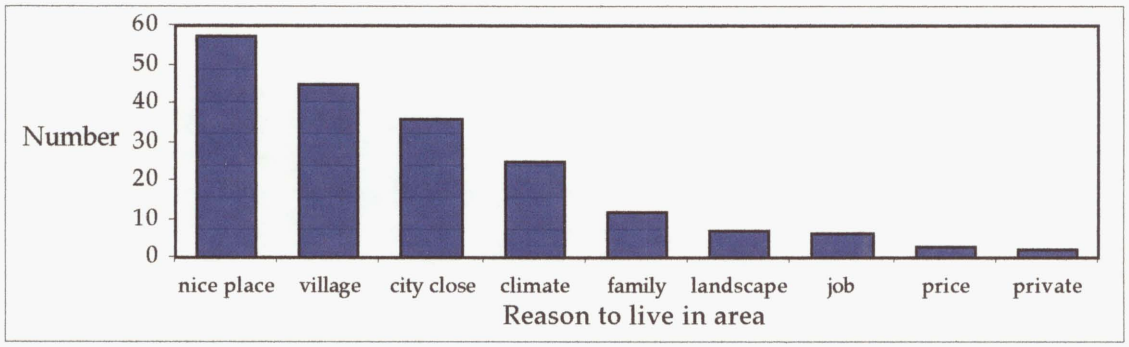
More people have visited Okuti Valley Scenic Reserve (about three quarters) than the neighbouring Birdlands Native Park Trust (about half), possibly due to the entrance fee at Birdlands. The Reserve is also visited more frequently. Respondents were informed that Okuti Valley Scenic Reserve is a totara/matai forest with an area of regenerating totara and matai under kanuka and asked why they like the Reserve. Reasons were equally spread between being a good example of totara/matai forest, having abundant birdlife, and being a place for walking.

Several comments were received concerning the small size of remnants and amount of native forest remaining in the area and the need for corridors between forest areas.

Figure 12.1 Okuti Valley study area, questionnaire results.

How long have you resided in the Okuti Valley / Little River area? (n=64)

Why do you live in this area (tick as many as you like)? (n=64)



Are you involved with any of the following in this area (tick as many as you like)? (n=64)

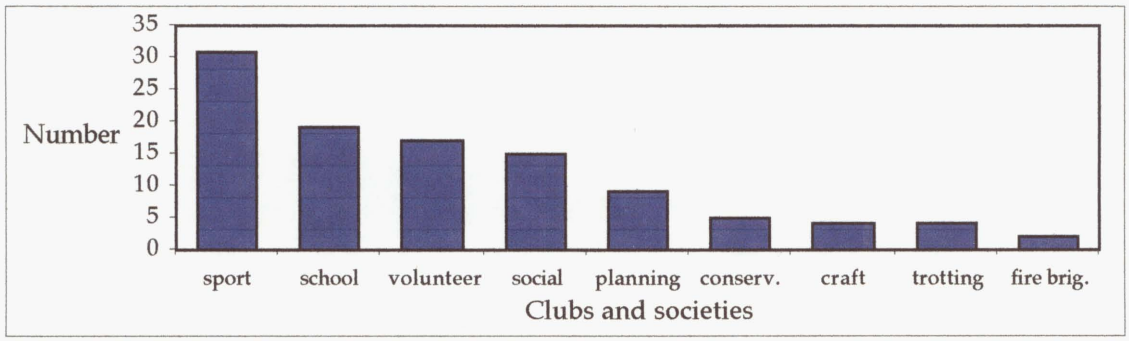
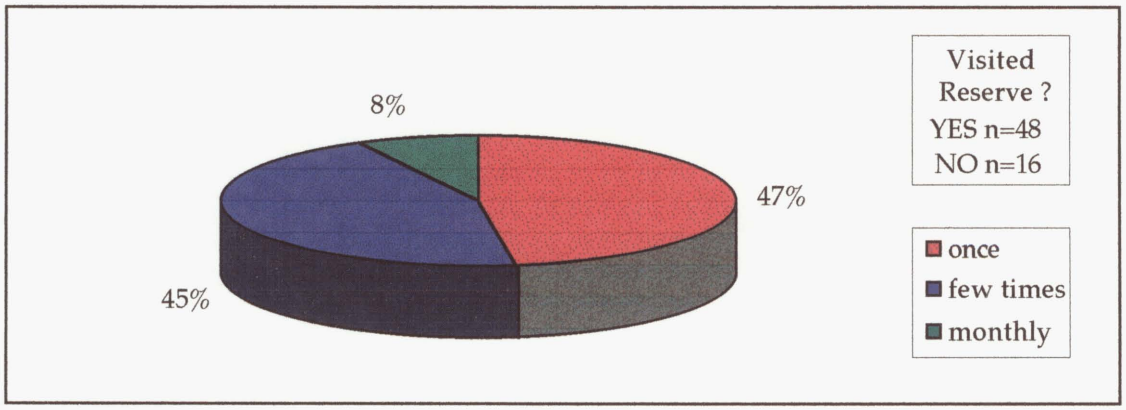
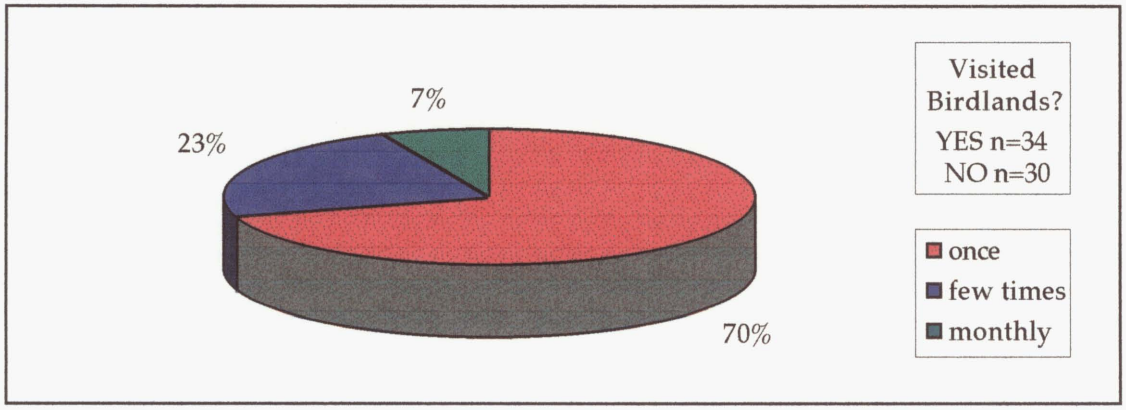


Figure 12.1 Okuti Valley study area, questionnaire results continued.

Have you visited the Department of Conservation Scenic Reserve in Okuti Valley Road (Okuti Valley Scenic Reserve)? If yes, how often did you visit this reserve in the last year? (n=64)



Have you visited Birdlands Native Park Trust in Okuti Valley? If yes, how often did you visit in the last year? (n=64)



12.4.2. Land owner attitudes

Land owner attitudes to trees in the landscape and land management appear in Figure 12.2. Perceived benefits of exotic trees are generally more selfish than for native trees e.g. for income, timber, privacy, and shelter. Native trees were perceived to be of benefit in the more holistic categories such as erosion control, aesthetics, bird habitat, waterway protection, and forest regeneration. Native trees were also considered to be of value for cultural heritage and tourism potential.

Attitudes towards funding providers for regeneration of native forest and erosion control plantings were similar. Most people thought land owners should be

responsible for the funding of these plantings as the land owners are responsible for the land and probably removed the forest cover in the first place, leading to erosion. More people thought that regeneration funding should be provided by Regional and National Government than erosion control plantings as it was of benefit to the whole country whereas erosion was perceived as primarily a land owner problem.

Several suggestions were received concerning erosion control planting funding:
- Erosion-prone land should not be stocked
- Landowners should pay if erosion was due to poor management
- Local Council should assist in planning and subsidise nursery stock
- National Government could provide tax incentives to plant for erosion control
- National government could fund or loan finances for plantings and then receive a proportion of profits when trees felled

Suggestions and comments were also received concerning forest regeneration funding:
- Regional Council experts can advise land owners on plantings and then have their fee refunded when trees are purchased
- National Government should legislate for regeneration and provide subsidies or tax incentives
- Concerns were raised over giving up private land for regeneration and public use although tittles could be retained through the use of covenants and trusts
- Many areas would regenerate by themselves if fencing was provided

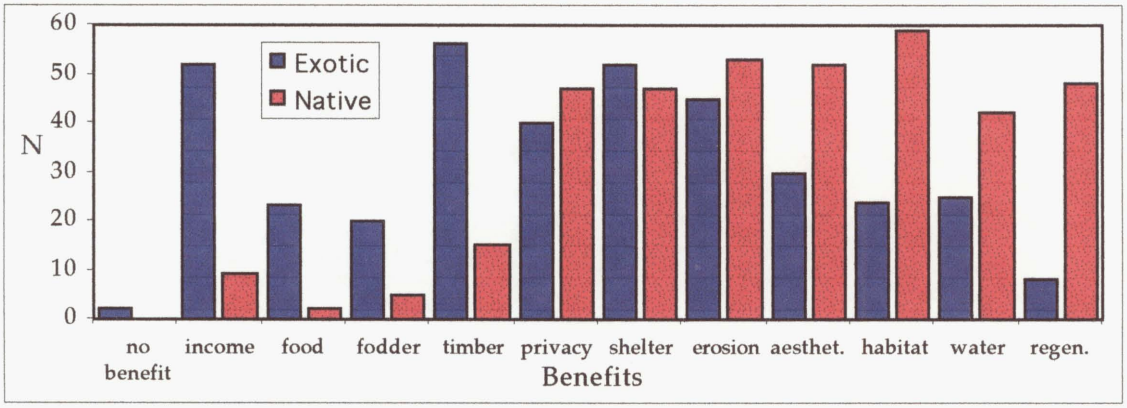
Respondents were asked whether or not they thought an integrated landscape management approach at the catchment level (combining erosion control, aesthetic plantings, diverse land use etc.) would be of benefit to themselves and the community. More people thought that this approach would be of benefit to the community (87%) than to themselves (78%). The need to explain the financial and aesthetic benefits to farmers was suggested, as well as the use of both natives and exotics until scientists develop faster growing natives.

Nearly half of the respondents (n=29) said that the land management practices of their neighbours affected them. Main effects ranged from water use (neighbours upstream using too much water), trees planted in the wrong place (blocking sunlight), spraying with chemicals or lack of weed control, and having unproductive bare land. Other effects were rabbits, poor erosion control,

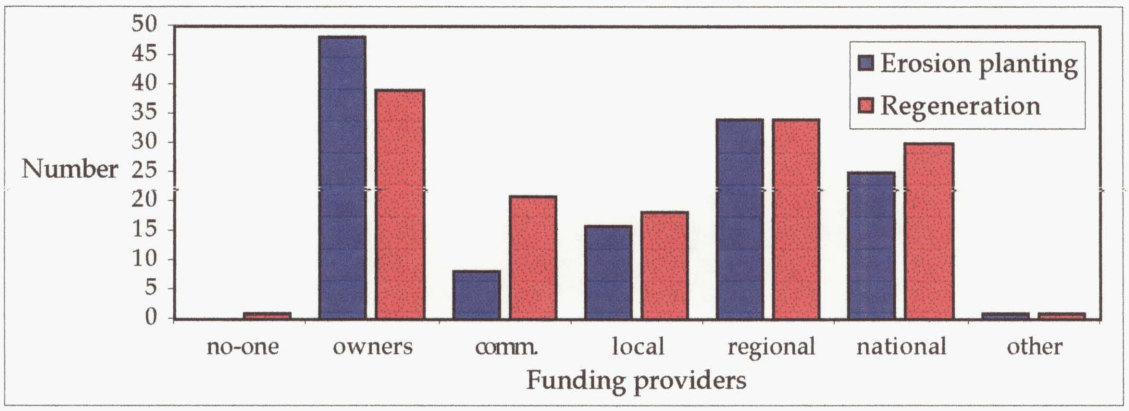
wandering stock, and the keeping of horses. An integrated land management plan may help in the amelioration of these effects between neighbours.

Figure 12.2 Landowner attitudes to trees in the landscape and land management, questionnaire results.

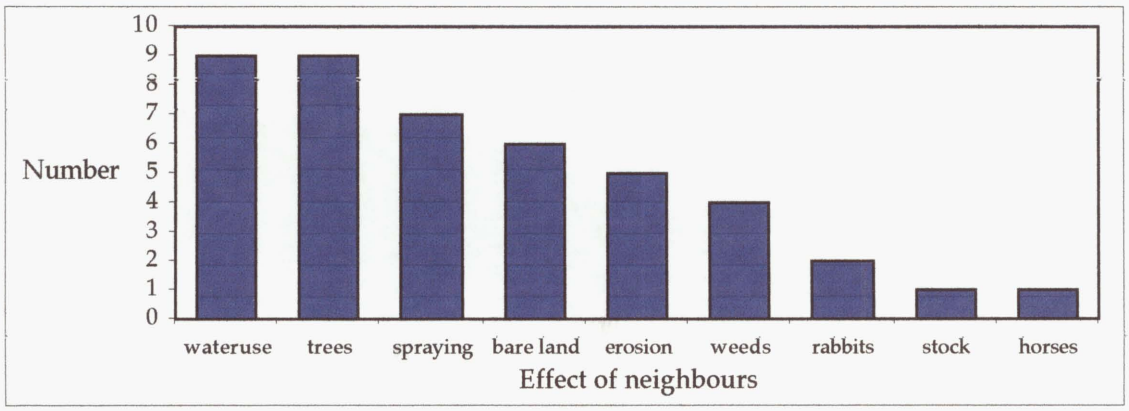
In general, what do you consider to be the benefits of planted trees? (n=64)



Who do you think should provide funding for the regeneration of native forest and the planting of erosion control trees on private land in the Little River and Okuti Valley areas? (n=64)



Do the land management practices of your neighbours affect you? (e.g. spraying, planting, water use etc.) If yes, in what ways? (n=29)



12.4.3 Land use

Questionnaire respondents were asked a variety of questions concerning land use, both present and potential. Attitudes to the amount of tree in the landscape, both exotic and native, were also determined. Questionnaire responses concerning land use appear in Figure 12.3.

Over 50% of respondents live on blocks of land less than 5 hectares, although 16% live on blocks greater than 100 hectares. Main productions are stock, garden produce, orchard crops, and timber. Three tourism ventures are present and two nurseries.

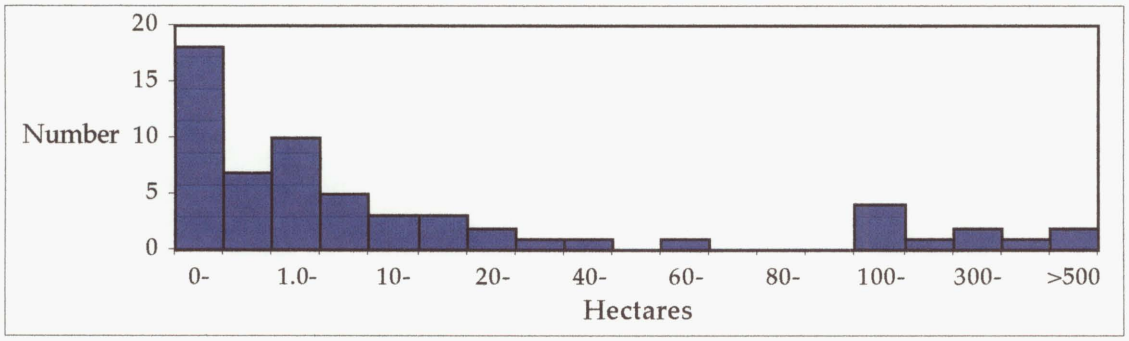
When asked as to what land uses people would consider given adequate finances, popular answers included timber production, erosion control and waterway protection plantings, and forest regeneration. Erosion control cropped up in several areas of the questionnaire and appears to be a major concern for people in this area.

When asked about the amount of exotic plantations and native forest (including kanuka) in the area, 77% thought there were not enough natives although three people considered kanuka to be a weed on their farms. The harvesting of kanuka for firewood was widely accepted to be an existing land use right although 10% of respondents were opposed to this. Concern was raised as to retaining economic viability while increasing native forest. Possums were also a concern.

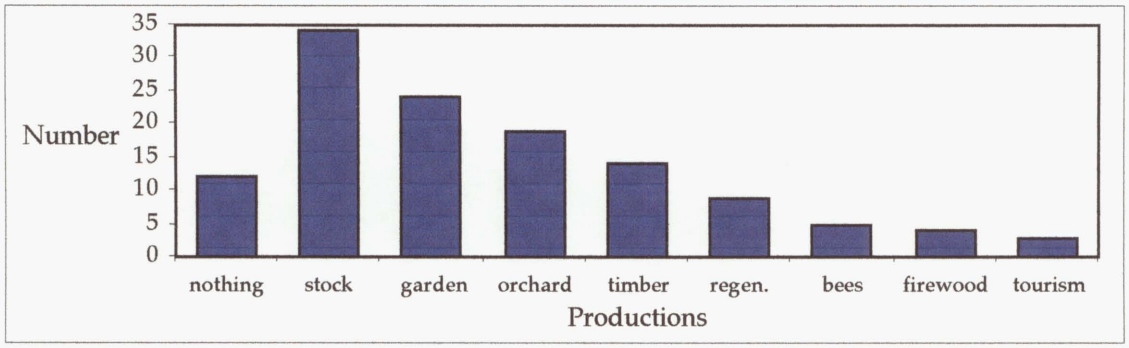
Opinion as to the amount of exotics was spread throughout all categories. Several people thought that a wider variety of exotics should be planted (e.g. orchard trees, Tasmanian blackwood, walnut) but not in plantations or on good farming land. Gorse was considered a major problem although one respondent said that pines suppress gorse. Economic benefits were raised as a reason for exotic plantations.

Figure 12.3 Land use and forest extent, questionnaire results.

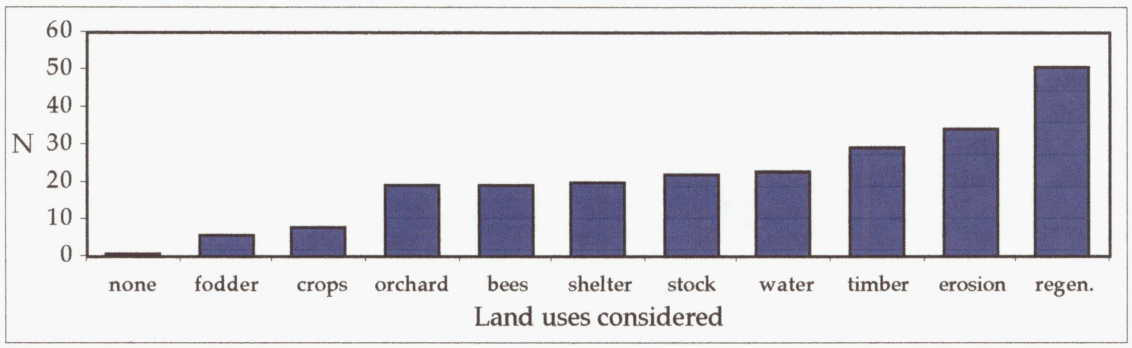
How large is the land you occupy? (n=61)



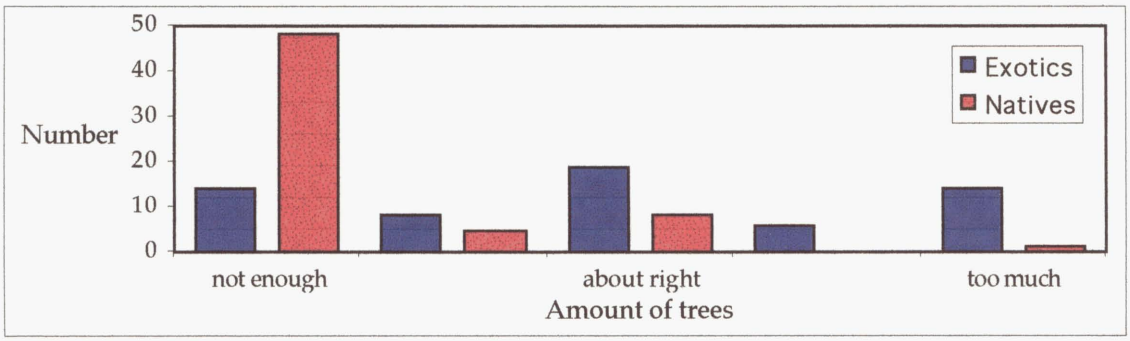
What is produced on the land you occupy? (n=64)



If the finances were available, which land uses would you consider? (n=64)



What do you think of the amount of exotic plantations and native forest?



12.4.4 Forest extent change

The extent of forest change over 50 years is shown in Figure 12.4 (A. Native forest and scrub. B. Exotic plantations and windbreaks etc.) and hectare values given in Table 12.1.

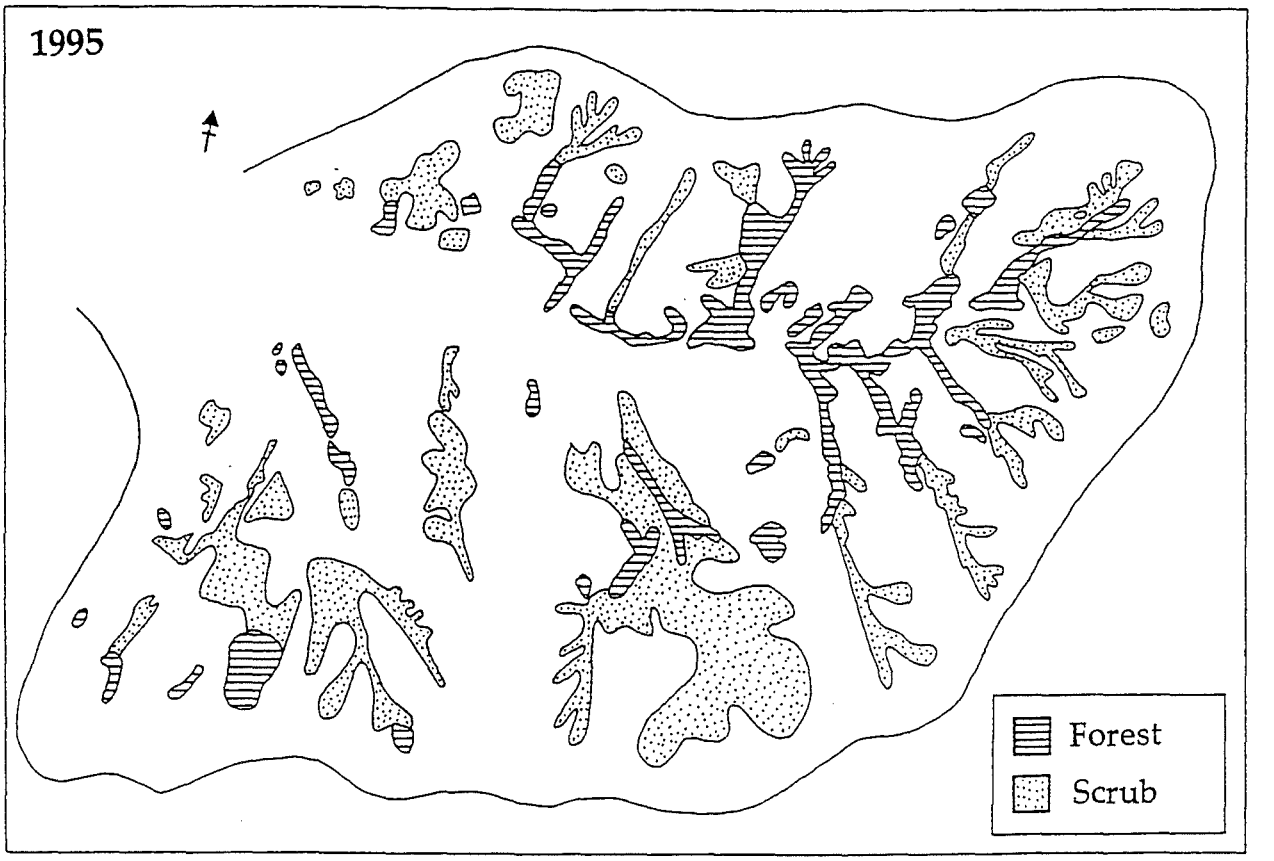
Table 12.1 Extent of forest change (hectares) over 50 years (1945 - 1995), Okuti Valley, Banks Peninsula.

YEAR	Native forest	Native scrub	Plantations	Windbreaks etc.
1945	530.6	1361.9	332.5	50.3
1995	689.0	1500.6	518.1	113.8
change	+30%	+10%	+56%	+117%

All forest types have increased from 1945 to 1995. Windbreaks and garden plantings have more than doubled in extent, exotic plantations have also increased significantly (see Figure 8.4B). Mainly north-facing slopes in the western reaches of the catchment have been utilised for exotic plantations. The 1945 aerial photograph shows many areas of soil slip erosion, possibly a result of the wholesale forest clearance of the catchment some 100 years earlier.

The native forest pattern is more complex. Some areas of scrub in 1945 have become forest by 1995 and vice-versa. In general native forest and scrub has become more fragmented through time, particularly in the western plantation area and the eastern-most farmland. Some pockets of scrub have extended in area and this accounts for the small overall increase through time.

Figure 12.4 Diagram of extent of forest change over 50 years (1945-1995), Okuti Valley. A. NATIVE FOREST AND SCRUB.



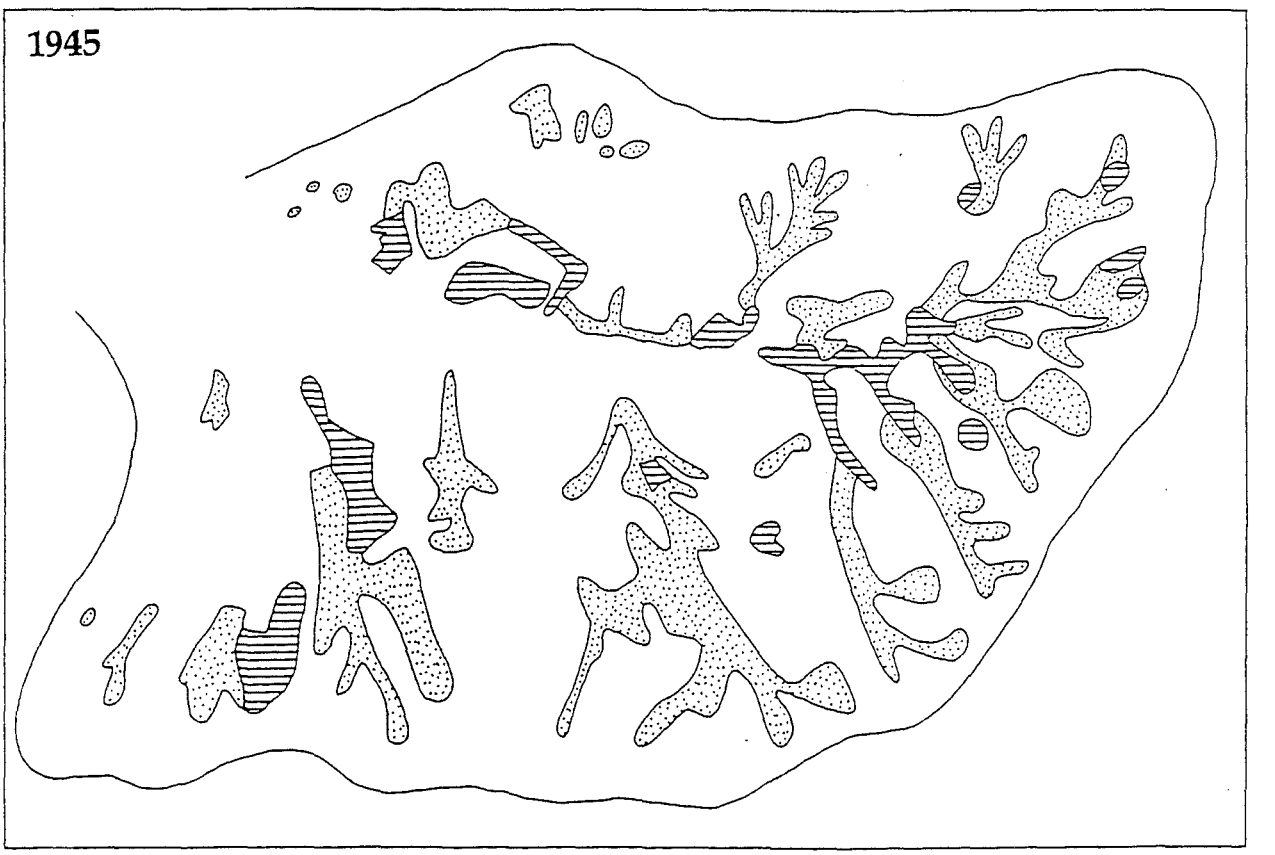
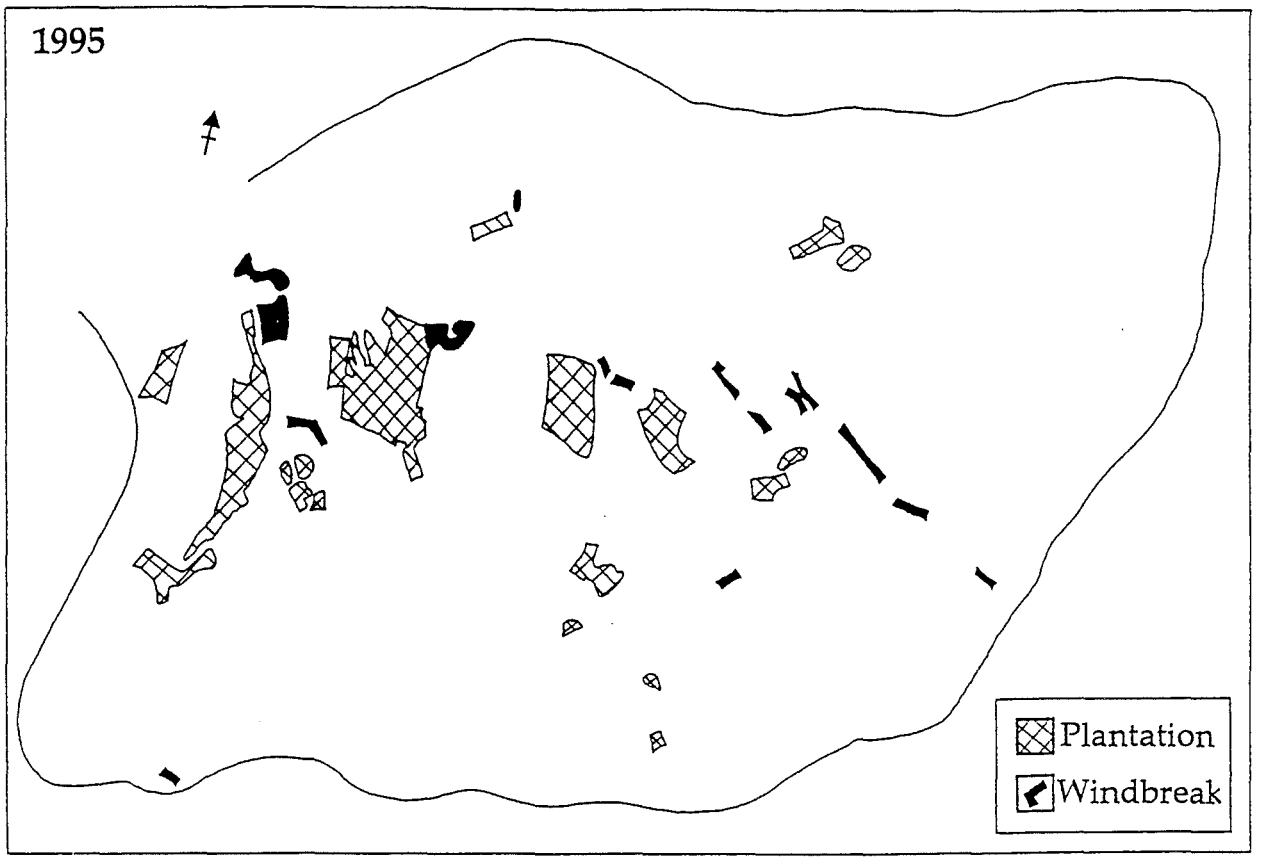
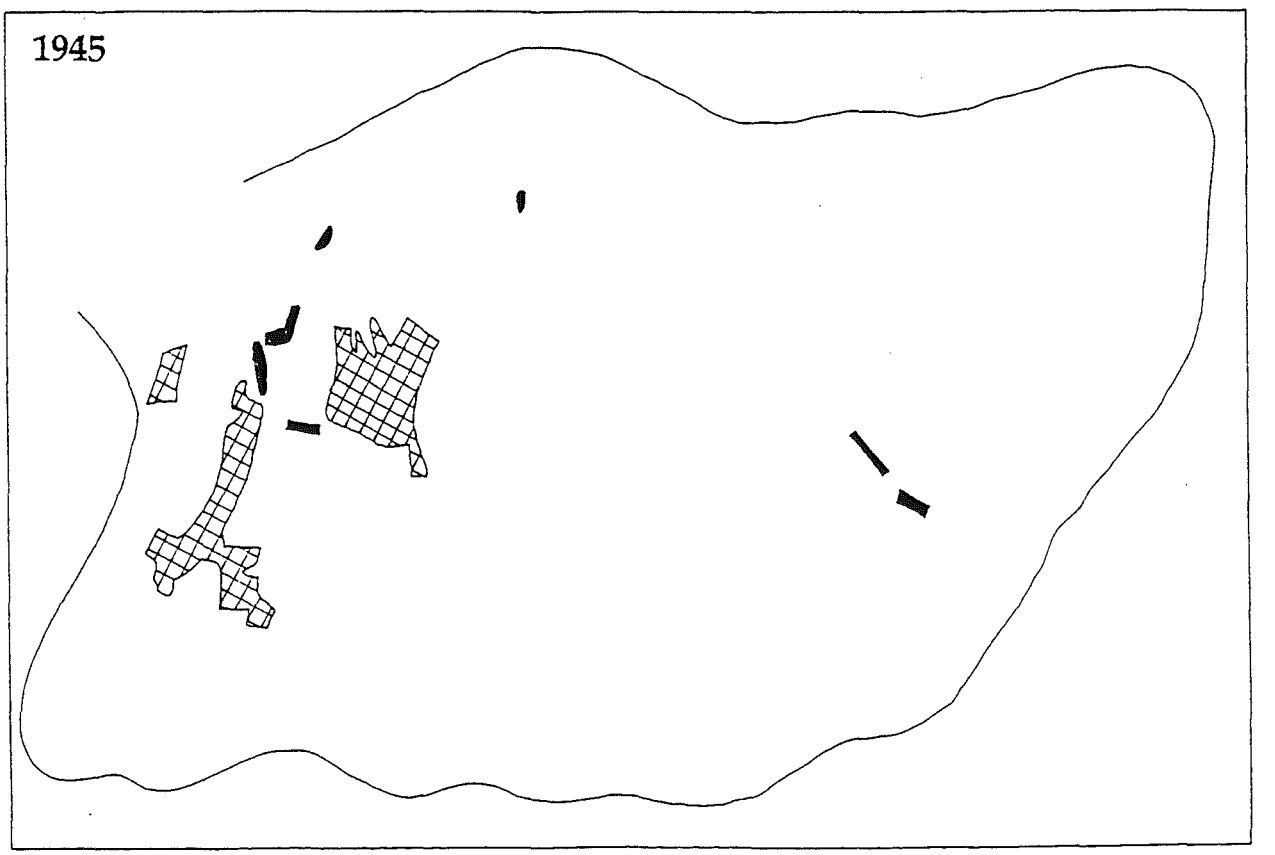


Figure 12.4 Diagram of extent of forest change over 50 years (1945-1995), Okuf Valley. B. EXOTIC PLANTATIONS AND WINDBREAKS.





12.4.5 Okuti Valley Landscape parameters

Landowner boundaries appear as an overlay in Figure 12.5 on the Okuti Valley topographical base map with Land Resource Inventory classifications. Land titles are generally large (in the order of 10's to 100's of hectares), with smaller residential blocks in the valley floor. Boundaries on the southern slopes tend to be less geometric than the predominantly rectangular pattern seen on the northern slopes.

Rainfall is circa 1000-1500mm per annum with more at higher altitudes (NZMS 1983). Slopes are compound and range from 2^0 to greater than 35^0 (MW&D 1975). Altitude ranges from 0 to 815m above sea level. Potential land use and soil conservation measures are identified.

Table 12.2 Land Resource Inventory classifications for the five areas in Okuti Valley, shown in Figure 12.5 (data from MW&D 1975, Van Berkel 1984). No. = Land Resource Inventory classification.

No.	SOIL TYPE	SLOPE	EROSION TYPE
1	recent alluvial	$0 - 3^0$	stream bank
2	yellow-grey - y-brown earth	$21 - 35^0$	moderate soil slip
3	brown granular loam	$21 - >35^0$	slight soil slip & sheet
4	upland yellow-brown earth	$16 - 35^0$	slight sheet
5	upland yellow-brown earth	$16 - 25^0$	slight sheet

Land Resource Inventory classifications for the five areas in Okuti Valley appear in Table 12.2 (data from MW&D 1975, Van Berkel 1984). Classification number 1 occurs on a floodplain at the western extreme of the catchment and is the most restricted in extent. Potential land use for this fertile area includes cropping and intensive grazing although flooding may occur.

Number 2 classification includes all of the Okuti valley catchment below circa. 300m. Present land use includes housing, mixed plantings, exotic forestry, and grazing. This semi-fertile area has compound slopes, some steep, and potential uses include grazing and production forestry. Soil conservation measures recommended to prevent soil slip include conservation fencing, oversowing and topdressing, and space planting (dotted trees). Scrub reversion is noted as a problem but for the purposes of the present study it is seen as an advantage. Okuti Valley Scenic

Reserve (totara/matai) and neighbouring Birdlands Native Park Trust occur in this zone.

Number 3 classification includes all of the Okuti Valley catchment from circa. 300 - 700m. Present land use is mostly grazing, although some areas are in forestry and some areas are reverting to scrub (bracken/gorse/kanuka/broadleaves). Potential land use is the same as current land use. Te Oka Scenic Reserve occurs within this altitude band.

Number 4 and 5 classifications are similar and occur on the catchment summits. Soils are relatively infertile and current land use is grazing. Potential land use is identified as grazing and production forestry. Soil conservation measures include oversowing and topdressing of eroded areas and gully erosion control. Vegetation is predominantly tussock, bracken, matagouri, and occasional Hall's totara.

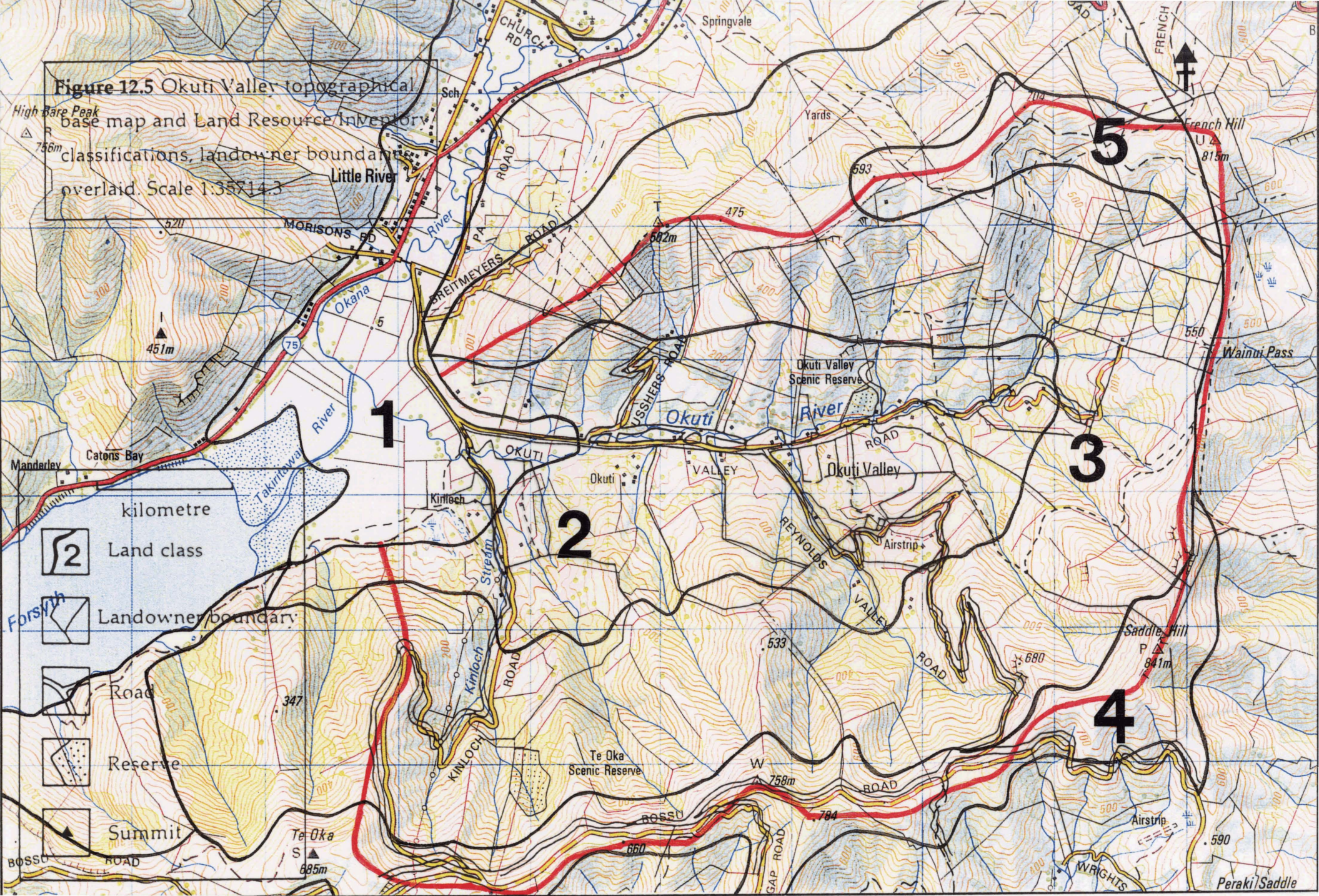


Figure 12.5 Okuti Valley topographical base map and Land Resource Inventory classifications, landowner boundaries overlaid. Scale 1:35714.3

12.5 INTEGRATED LANDSCAPE PLAN

Landscape patterns are a result of primary physical heterogeneity and secondary biotic heterogeneity (Hansson et at 1996). The existing biotic pattern in Okuti Valley is one of mainly plantations in the west and fragmented forest in the east (see Figure 12.4). Highly fragmented native forest mainly occurs as small strips with high perimeter to interior ratios. Contrast between vegetation types is generally severe (see Plate 17) with forest remnants occurring in an agricultural matrix. Connectivity between native forest and scrub areas has decreased since 1945.

The integrated landscape management plan for the Okuti Valley catchment appears in Figure 12.6. All suggested vegetation units are based on the primary physical pattern (topographical position and altitude) with the biotic pattern of the current vegetation overlaid. Vegetation units are positioned so as to provide connectivity between native forest and scrub areas. The shape of native forest and scrub units have been modified so as to reduce the perimeter to edge ratio. Practical considerations include the positioning of high intensity orchards near dwellings.

Forestry plantations are based on existing areas and areas suitable for forestry, i.e. steep upper slopes. Existing forest and scrub areas are used as nuclei for forest regeneration and corridors for bird movement are provided for. Lowland totara only occurs below circa 500m on the Peninsula and so forest types are divided into lowland totara dominated and upper slope (Hall's totara and broadleaves).

Erosion-prone gullies are recommended for regeneration and space planting (small groups of trees or widely spaced plantations) to protect both soil and water quality. Valley floors are the most fertile soils and are set aside for both garden and lowland totara forest regeneration (expanding outwards from existing remnants). Existing house sites are used as nuclei for more intensive garden plantings. The balance of land area which is not as erosion-prone, and therefore recommended for regeneration, is designated for grazing and space planting.

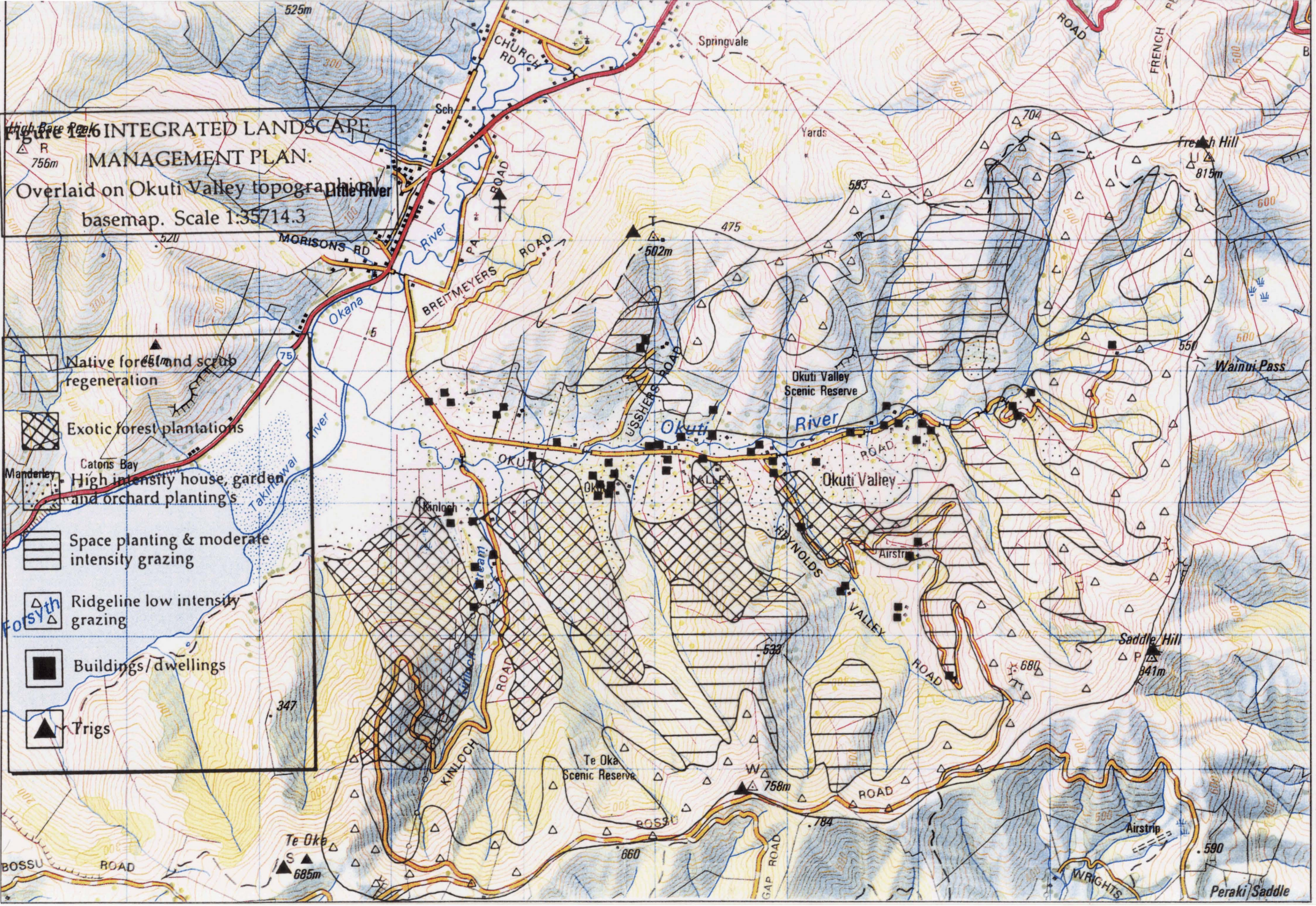


Figure 12: INTEGRATED LANDSCAPE MANAGEMENT PLAN.
Overlaid on Okuti Valley topographical basemap. Scale 1:35714.3
Native forest and scrub regeneration
Exotic forest plantations
High intensity house, garden and orchard plantings
Space planting & moderate intensity grazing
Ridgeline low intensity grazing
Buildings / dwellings
Trigs
Springvale
Okuti Valley
Okuti Valley Scenic Reserve
Te Oka Scenic Reserve
Wainui Pass
Saddle Hill
Peraki Saddle
Airstrip
Little River
Okana
Okuti River
Takiritawai
Kinloch
Forsyth
Manderley
Catons Bay
CHURCH RD
MORISONS RD
BREITMEYERS ROAD
USSHERS ROAD
REYNOLDS VALLEY ROAD
KINLOCH ROAD
BOSSU ROAD
WRIGHTS GAP ROAD
FRENCH ROAD
502m
815m
758m
685m
841m

The landscape management plan is divided into 5 units, options for landowners and suggested planting regimes are outlined below.

Native forest and scrub regeneration

Both native forest and scrub have increased in total area in the last fifty years. Local residents would generally like to see more native species in the area. Provision has been made in the landscape plan for the regeneration of native forest, mainly through the fencing of existing scrub areas or bordering the area with plantation or fenced space plantings with stock underneath. With time, these areas will develop into native forest with minimal landowner cost and effort (exclusion of stock, fire, and invasive weeds). The climate of the area makes it suitable for the 'no intervention' method - much of the Peninsula is reverting to scrub in the absence of grazing (pers.obs.). Fencing of remnants is strongly recommended. Stock will browse any native seedlings present and cause soils to become compacted. It is therefore vital that if any steps are to be taken to protect existing remnants, fencing is the first.

Corridors between forest remnants act to ensure the survival of the remnants (Bridgewater 1987) and are major conduits for wildlife movement. Corridors can be natural (riparian strips), remnant (left after fragmentation), or cultural (artificially constructed). Existing corridors need to be maintained, degraded corridors rehabilitated, and new ones established (Loney & Hobbs 1991). Some corridors between forest remnants exist in Okuti Valley, although more are required. The landscape plan (Figure 12.6) includes continuous tracts of scrub which should be left to regenerate to provide connectivity. Native scrub and forest areas which are not continuous have interplantings of tree crops or plantations to provide this connectivity. A riparian strip of native vegetation is also important to protect water quality (Banks Peninsula District Council 1997)..

Wilson (1994) has observed forest regeneration at Hinewai reserve on the eastern slopes of Banks Peninsula. The 'no intervention' method is used and many valuable observations have been made. Gorse rapidly reinvades land when grazing is ceased. Kanuka was seen to quickly out-compete gorse where both species establish concurrently. Under gorse stands older than about 10 years, the regeneration of shade tolerant native forest species is abundant. It is now accepted that gorse can provide a suitable nurse crop for the regeneration of native species if fire is totally excluded (Wardle 1991).

One method of revegetation which incurs a minimal cost is the broad-scale sowing of kanuka seed using kanuka slash (Porteous 1993). The kanuka nurse crop rapidly covers the bare ground and provides suitable conditions for the concurrent regeneration of the broadleaves and eventual canopy podocarps. The kanuka nurse crop can be thinned upon maturity to further release the forest species. Mature kanuka can be underplanted with native species to hasten forest development.

Provision has been made for continued harvesting of kanuka for firewood - several farmers stated that kanuka was a weed on their farms and the harvesting of kanuka was accepted as an existing land use right. Kanuka harvesting should be conducted in a selective manner i.e. thinning of older kanuka to release natives underneath. Kanuka and manuka (less common on the Peninsula) also provide bee fodder. Some people were concerned with the current practice of harvesting kanuka for firewood. Landowners are encouraged to investigate the use of exotic species such as eucalypts and wattles for firewood plantations.

Active revegetation can also be undertaken but at greater cost to the landowner. Species recommended for planting in the high land (above 500m) include Hall's totara, flax, *Hebe* sp., *Myrsine australis*, and *Coprosma* sp. Species suitable for the lowland areas (including river edges) are totara, matai, kahikatea, kowhai, cabbage tree, flax, mahoe, five finger, tree fuschia, marbleleaf, and *Coprosma robusta*. All of these species are native to the area and some also provide bee forage.

Avenues for investigation for landowners include QEII Covenants etc (see 11.5.3), discussions with local and regional Council, and the development of community based groups such as nurseries. Further information for landowners on revegetation techniques in a variety of situations and native forest restoration is available in Evans (1983) and Porteous (1993).

Exotic forest plantations

Exotic plantations for timber are limited to the western end of the catchment and the upper reaches where soil conservation is a priority due to the steep slopes. Woodlots should link into existing native vegetation to create an integrated vegetation framework, the boundary between the two being a mixture of species to avoid abrupt changes which look artificial. Exotic plantations should be tailored to fit the landscape rather than in unnatural looking geometric shapes (see Plate 18A). Planning and design guidelines for the planting of exotic trees in a way that will

enhance the landscape are available in Lucas (1989) and Banks Peninsula District Council (1993).

Landowners should consider the use of species other than *Pinus radiata* for timber tree plantations. Clark (1996) states that *Cupressus lusitanica* is a promising timber tree for Banks Peninsula. A boron deficiency is also noted for the Canterbury province and a topdressing of 4kg per hectare is recommended for improved tree growth. Other species include a variety of eucalypts and longer rotation hardwoods, such as firs and redwoods, with a higher eventual economic return. Longer rotation timber crops can also be planted as space plantings to prevent erosion. All of the above mentioned species are also suitable for shelterbelt plantings.

Plantation areas are surrounded by scrub and forest, garden plantings, and woodland areas. All of these vegetation types will aid in the prevention of siltation when the existing plantations are felled.

High intensity house, garden, and orchard plantings

The fertile valley floor has been allocated to high intensity house, garden, and orchard plantings. Due to the close proximity to houses, food crops should be the main species e.g. fruit and nuts. Species providing bee fodder should be included to enhance pollination and hence crop production. Exotic firewood species such as eucalypts and wattles grown in coppice are also suitable in this area.

Many options for landowners exist, the climate making the area suitable for a diverse range of food species such as walnut, hazelnut, almond, chestnut, pecan, nashi pear, olive, and sugar maple. Many of these species may provide an income. This area can also have small paddocks with high intensity grazing, or be allocated for pets, or manure producing animals such as chickens and pigs. Shelterbelts should be planted for multiple use - providing shelter, bee forage, stock fodder, wildlife habitat, and edible fruit. Shelterbelt plantings and hedges should avoid highly visible skylines and ridges and should aligh with existing landforms and edges of vegetation (Banks Peninsula District Council 1997).

One important area within this zone is the riparian strip along Okuti River. Ideally, this area should be planted with a thin strip of native species such as flax, cabbage tree, and other species suitable for the riparian microclimate and to provide food for native bird dispersers e.g. kereru. Run-off will be significantly reduced with

increased planting in the upper, erosion-prone, areas. The riparian vegetation will act as a final buffer zone to further protect water quality in the Okuti River.

Space planting and moderate intensity grazing

Areas recommended for space planting include steeper slopes and act as transition between grazing only on the ridges and plantation and forest areas. Tree crops offer the best medium for extending agriculture to hills and steeper land. Marginal hill country is less profitable for conventional farming and there is now more interest in tree crops and forestry. Tree crops give better productivity per hectare, especially when used in an agroforestry situation. After the initial establishment costs, the tree crops will provide for years with low inputs.

The New Zealand Tree Crops Association list the benefits of using tree crops as:

- deep rooting and so require less irrigation
- shelter for neighbouring crops and animals
- shade and fodder for stock and so increases productivity
- better pollination and fruit set as bees fly better in shelter
- tree shading improves moisture availability
- better ecological balance is created
- diversity increases plant interactions and biological controls
- leaf fall improves soil fertility through the accumulation of nitrogen and other essential nutrients for plant growth
- conserves soil moisture, prevents runoff and hence erosion.

Species providing timber and suitable for space planting include *Pinus radiata* but also a range of less common species such as Tasmanian blackwood, black walnut, and eucalypt. Hardwoods and specialty timber can also be grown as space plantings to provide a longer term income. Lowland totara can also be grown in these areas for eventual timber. Firewood production is also recommended in this area.

Fodder crops are an excellent choice for agroforestry situations as they are sited in the area were they are needed and will provide stock food during drought periods. Fodder trees suitable for the lowland (under 500m) include fodder legumes such as honey locust, carob, tree lucerne, and wattle. Exotic fodder species suitable for the lowland are chestnut, oak, poplar, and willow. Selection of willow species must be done will care as some are classified as invasive weeds.

Fodder trees suitable for the higher space planting areas (as well as the ridgeline) include fodder legumes such as honey locust, Siberian pea tree, tagasaste, and tree medick. Exotic fodder species suitable for higher land are chestnut, oak, and poplar. The multiple use of several of these species make them excellent choices for two-tiered farming. They provide shelter and food for stock, bee fodder, soil protection, landscape enhancement, and eventual economic return as a timber crop.

Landowners are advised to contact the New Zealand Tree Crops Association and the New Zealand Farm Forestry Association for further advice and information on the planning, planting, and maintenance of tree crops.

Ridgeline low intensity grazing

The Banks Peninsula District Council (1997) outlines forestry guidelines which include the avoidance of forestry development on visually sensitive ridgelines. The ridge line should be left to regenerate to its natural vegetation association (predominantly Hall's totara as open woodland over tussock and matagouri), space planted with hardwoods for long-term selective logging, or used for low intensity grazing (with or without space planting) to maintain the ridge-sky interface.

12.6 CULTIVATION AND RESTORATION OF LOWLAND TOTARA

Endemic New Zealand tree species are enjoying an increase in popularity for garden use. Metcalf (1991) discusses the use of podocarp species in the home landscape environment; lowland totara for specimen trees, *P.totara* cultivar "Aureus" for coloured foliage and indoor containers, and golden totara, snow totara, lowland totara, and *P.totara* cultivar "Aureus" for hedges and shelter purposes. The suitability of lowland and Hall's totara for soil conservation purposes is discussed by Pollock (1986). Both species are seen to prevent wind and sheet erosion.

Due to the greatly diminished extent of lowland totara dominated forest many workers have concentrated upon the artificial cultivation of totara to enable rapid reforestation of denuded areas. The performance of planted lowland totara on the basis of Forest Research Institute trials is discussed by James & Griffiths (no date), Pardy (1983a, 1983b), Beveridge, Bergin & Pardy (1987), and Bergin & Pardy (1990).

Beveridge et al (1987) state that lowland totara is easily established but can be coarsely branched partly due to frost and insect damage - Hall's totara is

considered to have a better form and less foliage damage at altitudes above 550m in the central North Island. Millett (1987) states that lowland totara is about the only native that can compete with exotics as a desirable farm tree. Thinning and pruning is suggested to improve tree form for timber purposes. The long time frame involved with growing natives for timber is somewhat ameliorated by the interim benefits of soil protection and landscape enhancement.

Lowland totara survival rates of 60-80% have been recorded for 20-50 year old plantations where shelter was provided and competing vegetation removed from around seedlings (FRI 1989). Totara is considered one of the fastest growing conifers in a plantation situation with a height of 17m and diameter of 61cm being reached after 60 years (FRI 1989) - a height similar to, and a diameter greater than, rimu and kauri. The suitability of totara for future timber production is widely accepted and the Forest Research Institute are currently conducting trials on the formation of heartwood under high growth conditions (Bergin & Pardy 1987).

With an increasing awareness of the value of forest remnants, and of the amount of impact that has occurred in New Zealand since human settlement, there has been a growing interest in attempting to restore our native forests. The large body of planting trials conducted by the Forest Research Institute has helped in providing information on how to conduct restoration projects in either cut-over or on bare land. Guidelines for the restoration of native species and their use in plantations have been prepared by the FRI (e.g. Beveridge et al 1987, Bergin, Pardy & Beveridge 1988) although little information exists concerning the artificial establishment of natural forest associations.

The above studies suggest the suitability of lowland totara for restoration and revegetation projects, and as a plantation timber tree. The severe reduction in the extent of lowland totara forest has had an impact on Maori, who venerate lowland totara for its carving properties. Local Maori are interested in the artificial establishment of lowland totara plantations for cultural uses (James Mason Russell pers.comm.) and these studies may help to provide useful information.

Results of the present study show the natural state of totara/matai/kahikatea associations and their spatial structure. These results can be used if approximation of the 'natural' state is the aim of revegetation projects i.e. the podocarps are planted so that their spacing is similar to that found in naturally regenerated stands. Number per hectare and mean spacing of adult podocarps in Banks Peninsula study sites is shown in Table 12.3.

Table 12.3 Number per hectare and mean spacing of podocarp adults in Banks Peninsula study sites. * = spacing not determined (minimum 4 adults in plot).

		Number per hectare			Mean spacing (m)		
STUDY SITE	FOREST TYPE	totara	matai	kahik	totara	matai	kahik
Price's Valley	matai	10	105	15	40.0	5.75	*
Okuti Valley	totara/matai	120	40	-	5.42	10.4	-
Okuti kanuka	totara/matai	117	50	17	5.43	*	*
Peraki Saddle	totara/matai	57	20	-	6.86	9.1	-

The amount of each podocarp species depends upon which forest type should be present in an area i.e. fertile alluvial plains (e.g. Price's) will be more matai with scattered totara and kahikatea, alluvial terraces (e.g. Okuti) will be predominantly totara/matai with scattered kahikatea in wet areas, and the less fertile colluvial slopes (e.g Peraki) will be totara/matai. The colluvial slopes also have the added dimension of an altitudinal effect which sees the increasing abundance of Hall's totara above circa 450m. All sites where totara/matai/kahikatea are encountered show totara to be spaced at circa 6m and matai circa 10m. The almost pure matai stands should have matai at circa 6m spacings and totara scattered throughout at greater spacing.

12.7 DISCUSSION

New Zealand's natural environment has been radically altered in the last 150 years. Wholesale forest clearance has had a disproportionately high impact on all lowland forest types. Lowland totara dominated forest is now highly fragmented due to its position on prized fertile soils. The spread of pastoral and agricultural practices have reduced the area available for colonisation and hence the future survival of lowland totara dominated forest.

The most important form of disturbance which acts to initiate cohort regeneration of lowland totara dominated forest appears to be flood events, i.e. river course changes, deposition events that may be earthquake-triggered. Humans have significantly altered the natural disturbance regime with the prevention of fire, alteration of river courses, and acceleration of erosion processes. Lowland totara does not appear to regenerate under a senescent canopy and so in the absence of

the natural disturbance regime, provision must be made for all regeneration stages of lowland totara if its future survival is to be assured.

Many lowland forest remnants may be "living museums" and without adequate animal pest and introduced weed control forest composition may alter drastically (Ogden 1995). Restoration and revegetation is therefore an option for the future survival of lowland totara. The suitability of lowland totara for use in plantations has been determined. Silvicultural plantations can provide timber (totara heartwood being highly prized), income, and seed sources for regeneration. Land values such as water and soil quality will also benefit from artificial plantations.

In New Zealand, there is a growing interest in sustainable forms of land use other than the traditional non-sustainable forms which are largely based on monocultures of ryegrass - white clover and *Pinus radiata*. Net returns from livestock products have fallen, bringing about an interest in other forms of land use involving new animals, crops, and products.

Examples of integrated landscape management are documented by Kubricki et al (1993) and Bradby (1991), who suggest that greater funding support for community-led initiatives is the most effective way of enhancing corridor networks. Human responses to environmental problems are discussed by Lefroy & Hobbs (1993) and range from ignorance and denial to technological optimism. A change in paradigm to take in a wider view of nature and our relationship with it is suggested.

The New Zealand Sustainable Land Management Strategy (Ministry for Environment 1996) regards the voluntary actions of landowners to carry out better land management practices as the best way to achieve the environmental improvement required. A major emphasis of the strategy is on providing information and support in a form that will encourage land users to change their unsustainable practices.

Couper (1993) suggests that farmers need to rehabilitate their land to protect soils and remaining natural heritage, and that there is a need for better scientist-farmer interaction. Couper (1993) states that if farmers are to be persuaded to rehabilitate their land and adopt conservation measures that will lead to sustainable land use then the following criteria need to be met:

- need to be affordable in terms of initial cost and financial benefit

- need only minimal care after establishment
- have a potential to produce income (timber, seeds, oil etc.)
- have a demonstrated ability to increase yields, profits, and value of the land
- have the support of local Government, neighbours, and community
- have incentives from National Government
- must be integrated with all other conservation measures in the area.

Many of the above criteria were identified from the questionnaire results. Proper land management planning should act to meet many of these criteria.

Saunders et al (1987) state that there is a persisting perception in the community that forest remnants are merely unproductive areas of bush. They state that this perception should be changed and that a new approach to land management is required, based on sustainable production and takes into account the values of remnants to production. They suggest that farmers would then accept a greater responsibility for ensuring that local remnants are preserved.

Park (1980) suggests that greater scientific attention should be directed towards information that informs the landowner and stimulates the protection of private land through Open Space Covenants etc. The importance of involvement by scientists in the public education process is also echoed by Erlich (1993). He states that the entire population of the planet must be involved in the development of sustainable land management practices or else our other efforts are doomed to fail.

From the current knowledge of landscape interaction we now see that an holistic strategy is required to ensure the long-term viability of our fragmented forests, i.e. an integrated landscape mangement strategy. It is therefore vital to apptraoch landscape management on a scale appropriate for all land use, including provision for the continued regeneration of fragmented forest species such as lowland totara.

The restoration and revegetation of totara dominated forest is particularly important in the Okuti Valley catchment as small remnants mainly occur as square areas within a pastoral matrix, making them vulnerable to the external influences of a fragmented landscape. Past land use has resulted in soil compaction (from stock trampling) and alteration of the natural disturbance regime (river changes due to accelerated run-off and human settlement). Large-scale river changes may now not occur in this catchment and so the future survival of lowland totara may depend on active management.

The future regeneration of lowland totara is provided for in the example integrated landscape management plan, where existing forest remnants are used as nuclei for spread into surrounding scrub areas. Existing land uses remain and a modified agricultural system is presented. While the presented landscape management plan is an example only, it could be used as the basis for further discussion with landowners concerning the future management of the catchment. I would suggest that the catchment level is an appropriate scale on which to address the fragmentation problems of many of our native forest species. Approaches based on species ecology, social, and environmental considerations provide an effective way of managing fragmented landscapes and for improving the biological conservation of lowland totara while allowing for other land uses.

Plate 18 Recent Banks Peninsula exotic plantations; (A) *Pinus radiata*, Kaituna Valley, (B) *Eucalyptus* sp. Okuti Valley.

A

B

CHAPTER THIRTEEN
CONCLUDING DISCUSSION

13.1 LOWLAND TOTARA IN SOUTH ISLAND

Since the first fires associated with early Polynesian settlers some 800-1000 years ago (McGlone 1983b) burning, logging, and clearing for settlement have substantially reduced or modified New Zealand's forests. The extensive deforestation that accompanied Polynesian and European settlement of New Zealand has had a disproportionately high impact on lowland podocarp forest, with the majority gone and only surviving today in isolated remnants of generally small size. Blaschke et al (1981) estimate the amount of lowland podocarp and podocarp-hardwood forest presently remaining in New Zealand to be 3.3% of the land surface. Lowland podocarp forest is significantly under-represented in New Zealand's reserve system and there are very few examples of totara dominated forest remaining in New Zealand (e.g. Park & Walls 1978, Thompson et al 1980).

Figures for specific regions of New Zealand indicate that lowland totara has been reduced to approximately 1% of its original distribution (Esler 1978, Johnston 1969, Wilson 1992, McSweeney 1982). The extremely limited extent of lowland totara dominated forest means that it is important to understand the ecology of this forest type in its natural environmental niche, and to ensure its future survival within the now highly fragmented New Zealand landscape.

Chapter Two contains a full review of the literature relating to lowland totara. Gaps in the knowledge base are identified and used to determine the research approach of the thesis. Chapter Three details study site selection, data collection, and tree ageing methodologies. The objectives of this chapter were to ensure adequate coverage of geographical location and climate in the northern half of South Island, to ensure adequate coverage of a range of landforms and soils, and, to ensure adequate coverage of all lowland totara forest types and development status.

Chapter Four outlines the distribution and niche requirements of lowland totara.

Data on current distribution, study site climate and landform, and study site soils are given. Lowland totara would have occurred throughout all ecological districts of lowland New Zealand under 500m, the most dense stands occurring on fluvial deposits with relatively fertile soils; alluvial terraces and fans, river plains, and coastal dunes. Totara would have dominated on the free-draining gravel soils and kahikatea on the silt soils. In New Zealand, naturally fertile soils are of limited extent (Wardle 1991), examples being recent, fine-textured alluvial soils (such as on the river plain at Coke Covenant), and colluvial soils derived from basaltic or calcareous rocks (such as at Blue Duck Scenic Reserve). Totara dominated forest would therefore have been correspondingly limited in extent. The occurrence of totara forest on fertile soils made them prone to destruction by farming pioneers.

In South Island, totara mainly occurs within the 800 - 1600mm rainfall isohyet, except for northwest Nelson and Westland where rainfall is higher. In North Island, totara occurs within the 800 - 1600mm rainfall isohyet in the Wellington and Auckland regions. Elsewhere in North Island totara mostly occurs in the 1600 - 3200mm rainfall band. The general trend in New Zealand is for temperature and humidity to increase with rainfall and so for Nelson and most of North Island, elevated temperatures and humidity levels would allow totara to dominate whereas in the remainder of the country totara is limited to the lower to mid rainfall regions.

Lowland totara is replaced by Westland totara (*P.totara* var. *waihoensis*) on the west coast of South Island. Westland totara occurs throughout Westland with an annual rainfall of 1600 - 6400mm. Trees do not reach the height of true lowland totara, which reflects the origin of this stable hybrid (*P.totara* x *P.acutifolius*); *P.acutifolius* is a shrub. Altitude has an effect on the totara species present - Hall's totara replaces lowland totara above circa 450m. Hybrids commonly occur between the two species, particularly around this altitudinal zone.

The distribution of lowland totara dominated stands is a function of several interlinked site characteristics such as climate, landform, drainage, disturbance regime, and soil type, with an altitudinal limit superimposed. Lowland totara appears to be confined to semi-fertile or fertile soils which are the result of landform and disturbance, i.e. flood events on a river plain.

Chapter Five discusses the disturbance history of the study sites and determines the importance of disturbance for the regeneration of lowland totara. Likely disturbance regimes of each study site were identified. Regeneration was seen to

occur in canopy gaps, on flood surfaces, following fire, and on prograding dunes. Disturbance regimes favouring the regeneration of lowland totara dominated forest therefore appears to be in the medium to catastrophic range.

Chapter Six provides in-depth descriptions of lowland totara dominated stands. Study site forest types, descriptions, and age class frequencies are given. Totara dominated forest is a distinct lowland forest type, occurring on catastrophically-disturbed, free-draining lowland sites. Stands studied in this project, and where they predominate, range from pure totara to totara and all of the other podocarps. Communities found are classified below, although they intergrade:

1. Totara/matai/kahikatea/rimu/miro (dense mixed)
2. Totara/matai/kahikatea
3. Totara/matai
4. Totara

The podocarps have differing nutrient, light, and disturbance regime requirements and these factors work together to partition the environment into optimal areas for the regeneration and persistence of each species. Totara, matai, and kahikatea occur on more fertile soils than rimu. Totara and matai occur on better drained soils whereas kahikatea can tolerate water-logged soils. Totara and kahikatea dominate in catastrophically disturbed areas, miro responds to medium levels of disturbance such as tree fall, and rimu dominates in areas subject to continual disturbance such as canopy turnover.

Chapter Seven investigates seedling ecology. Studies on seedling distribution, spacing, and establishment are presented. Seedlings are preferentially distributed around or under both angiosperms and parent tress. Many seedlings show a clumped distribution, especially around angiosperms. The importance of high light levels for the regeneration of both totara and kahikatea is demonstrated. Catastrophic disturbance acts to remove the existing vegetation and hence elevate light levels. Nurse crops may play an important role in providing appropriate microclimates for podocarp regeneration. Matai is somewhat more shade tolerant and as such is late successional, i.e. totara and kahikatea enter the stand at the peak of light levels, matai can regenerate under lower light levels.

Chapter Eight investigates the spatial structure of lowland totara dominated stands. Analyses are applied to determine patterns, processes, and associations. Adults show examples of being repulsed from angiosperms, possibly because the

angiosperms present when the podocarp seedlings regenerated have since died. Spatial autocorrelation indicates that most stands studied are even-aged, regenerating as a result of medium to catastrophic disturbance.

Chapter Nine details temporal patterns in stand growth through an investigation of ring widths and stand growth. An understanding of the temporal development of totara dominated stands will help in the prediction of future stand structure and the classification of forest types. Generalised models of stand development and growth are proposed for totara dominated stands and can be used to extrapolate future stand development. Young/developing stands would be expected to continue their high growth rates until the canopy closes (180 - 200 years after stand initiation). Growth then slows to a steady low rate until individuals become emergent from the main canopy. Tree falls can also release individuals due to the increased availability of light.

Mature stands would be expected to maintain a steady low growth rate, associated with a continuous closed canopy, until individual tree falls occur to allow the remaining individuals to increase growth and take their place in the canopy (such as seen in Blue Duck). No seedlings or saplings were observed at Blue Duck and so the canopy openings, reflected by the released trees, may not have been large enough to allow the establishment of seedlings. In the absence of disturbance at Blue Duck, a canopy collapse process may well occur.

Dennistoun Bush huge is the only senescent stand in the present study. No evidence of regeneration under the opening canopy was observed. The occurrence of Dennistoun Bush huge on an active alluvial fan with catastrophic flood deposition events every 250 years seems to predispose this stand (and Denn 1 and 2) to periodic rejuvenation, resulting in a mosaic of first generation stands. Unfortunately, almost all of the large totara in New Zealand have been felled for timber and so the study of senescent stands, and their replacement, is difficult.

Chapter Ten is an overview of the ecology of lowland totara based on the studies performed in Part Two. With an understanding of the ecology of lowland totara, one can then address the future survival of this species. Regeneration is seen to be a consequence of seedling dispersal to preferred microsites, attraction to angiosperms, and disturbance history. The broad scale forest pattern is determined by the level of disturbance and the finer scale pattern of tree distribution is a result of light levels, parent and perch trees, and edaphic properties such as drainage and fertility. There is no evidence that the totara dominated stands studied here are

older than first generation, indicating that periodic catastrophic regeneration is required to re-initiate even-aged stands. The alteration of the natural disturbance regime by humans may pose problems for the future of lowland totara.

As totara dominated forest appears to be a first generation forest type, colonising disturbed areas and new surfaces, it is vital that areas are maintained for future regeneration. Landforms and soil types suitable for totara forest have been identified in this study. The most important form of disturbance which acts to initiate cohort regeneration of lowland totara dominated forest appears to be flood events, i.e. river course changes, deposition events that may be earthquake-triggered. Sea level change and human induced fire also provide new colonisation surfaces. Catastrophic disturbance must be allowed to continue and the resulting colonisation monitored for weed invasion. In the absence of catastrophic disturbance events, provision must be made for all regeneration stages of lowland totara. The future regeneration of lowland totara is provided for in the integrated landscape management plan, where existing remnants are used as nuclei for spread into the surrounding scrub areas.

There is no evidence that totara forest regenerates under a senescing totara canopy. Presently reserved areas are therefore likely to undergo floristic composition change away from totara/matai/kahikatea, possibly to increased angiosperm abundance, in the absence of disturbance. I would suggest that current reserves have their boundaries extended so that totara can regenerate around the edges. A landscape management plan is proposed as a mechanism for providing adequate areas for the long-term survival of totara dominated forest in the future by providing corridors for species movement and expanding existing forest nuclei.

Chapter Eleven contains a review of fragmentation literature as well as an example of fragmentation in an area which had extensive totara forest (Banks Peninsula). Data on forest reduction is presented.

Chapter Twelve presents an integrated landscape plan to provide for the regeneration of lowland totara in the future based on regeneration requirements for an area in Banks Peninsula. A questionnaire of landowner attitudes is presented as well as options for landowners to provide for the future regeneration of lowland totara. Other landuse issues such as soil protection are discussed.

New Zealand's natural environment has been radically altered in the last 150 years with the invasion of humans, exotic weeds, and introduced pests. Forest structure

in the future may reflect these invasions with resulting floristic change. Many lowland forest remnants may be "living museums" and without adequate animal pest and introduced weed control forest composition may alter drastically (Ogden 1995). Restoration and revegetation is therefore an option for the future survival of lowland totara. The suitability of lowland totara for use in plantations has been determined. Silvicultural plantations can provide timber (totara heartwood being highly prized), income, and seed sources for regeneration. Land values such as water and soil quality will also benefit from artificial plantations.

The present study provides a baseline for the 'natural' (i.e. pre-human) state of totara dominated forest. The ecological niche of lowland totara is defined and stand associations described. Stand spacing and age structure is determined and can be used in the future when revegetation projects have the aim of approximating natural stands. Methods of revegetation have been suggested and range from no intervention (with stock exclusion only), to the establishment of a suitable nurse crop, to active revegetation and planting schemes.

13.2 LOWLAND FOREST MANAGEMENT

The importance of lowland forest in the long term conservation of New Zealand's biological diversity is discussed by Park (1980) and Ogden (1995). Lowland forest, including totara dominated forest, occurs on high-nutrient soils and are ecologically, floristically, and faunistically distinct from other areas such as uplands, steeplands, and montane (Park 1980). It is widely accepted that larger forest patches contain more vascular species (Norton 1989, Norton 1996, Lavers & Haines-Young 1993). However, lowland forest contains more woody species than other areas (Ogden 1995) and even the smallest areas of lowland forest are considered important, as sources of seed and pollinators for future regeneration (Park 1980).

Many lowland reserves are considered too small for long term population survival without human intervention (Norton 1989). The future survival of lowland forest types is likely to be a function of adequate management and rehabilitation (Park 1980). Management options include passive management (i.e. do nothing) and active intervention (Norton 1988). The restoration and re-creation of lost and modified ecosystems should be seen as complimentary to the protection of those remaining (Atkinson 1988). The correct use of species of local origin in restoration and revegetation schemes is also important (Timmins and Wassilieff 1984).

Ogden (1985) suggests that a patch dynamic model is appropriate for many of New Zealand's canopy tree species. The present study concludes that lowland totara is a first generation forest type and requires relatively large scale disturbance events to create new surfaces for its colonisation. Pickett & Thompson (1978) suggest that reserves need to be large enough to include representation by all successional stages, which adds a temporal aspect to diversity. In New Zealand, most totara remnants are not large enough to allow for this recommendation. It is therefore vital that appropriate scales are used for land management i.e. regional or catchment level.

Traditional reserve management stops at the reserve boundary. From the current knowledge of landscape interaction we now see that a holistic strategy is required to ensure the long-term viability of our remaining natural areas i.e. an integrated landscape management strategy. The position of lowland forest on highly prized fertile soils makes them vulnerable to felling by pastoralists. This reduces the area available for colonisation and hence the future survival of lowland totara dominated forest. It is therefore vital to approach landscape management on a scale appropriate for all land use, including provision for the continued regeneration of lowland totara on catastrophically disturbed surfaces.

One landscape approach to management is the 'network' system advocated by several authors (Harris 1984, Forman & Godron 1986, Hobbs et al 1993b). Such a network would also contain linkages between other remnant areas, providing corridors for species movement across the landscape. The added advantage of managing a network of remnant areas and associated corridors is the opportunity for landscape restoration and reintegration. Adjacent denuded tracts may not only provide areas for regeneration of catastrophic disturbance requiring forest species such as lowland totara, but also have significant value in what they may become in the future.

The future regeneration of lowland totara is provided for in the integrated landscape management plan on a catchment level, where existing remnants are used as nuclei for spread into the surrounding scrub areas. The scrub areas, and forest edges, provide new areas for totara dominated forest to colonise. Long term survival of totara dominated forest will be enhanced if a shifting mosaic of successional stages is allowed to prevail. The present study addresses this by first determining regional pattern of forest distribution and then suggesting a method of land management on the catchment level to provide for the future survival of lowland totara within a predominantly pastoral matrix.

A new ethic for landscape management is rapidly evolving in the field of ecology. Species cannot be considered in isolation from their environment; social and economic factors also require integration into the overall land management plan. Molloy (1988) suggests the ecological ethic for tomorrow's land use should be based on the conservation of finite resources such as soil. Environmental common sense and economic sense should prevail when considering land use. The new landscape ethic is based on the following principles:

- Land use should be based on whole-ecosystem management.
- Planning should take into account extreme events as well as the average i.e. catastrophic disturbances of apparently regular occurrence.
- Aesthetics should be considered.
- A goal of sustainable yields of clean air, water, and produce. This suggests a move towards more use of organic practices and soil conservation measures.
- All costs should be counted in terms of not pushing production beyond the point of diminishing returns, such as found in current land use practices.

13.3 FULFILMENT OF RESEARCH AIMS

The two main aims of this thesis, research approach and their fulfilment, appear below.

1. To elucidate the ecology of *Podocarpus totara*

- Investigate literature concerning the ecology of *Podocarpus totara* and identify areas of knowledge which require further research. Literature review in Chapter Two outlines all current knowledge of lowland totara. Further research required is identified as; distribution and niche requirements, seedling growth and establishment, stand structure and development. All of these areas are addressed in the present study.

- Evaluate the current distribution and ecological niche of *Podocarpus totara* dominated communities in South Island, New Zealand. Determine potential pre-deforestation extent based on historical records and landform/vegetation relationships. Chapter Four defines the ecological niche of lowland totara, former extent, and extent of deforestation.

- Use rapid mapping techniques to determine stand history, regeneration requirements, forest associations, stand development and structure. Chapter Six

outlines general stand descriptions and forest associations, Chapter Seven seedling establishment and growth, Chapter Eight stand development and Chapter Nine growth through time. Generalised models of podocarp niches and stand growth through time are presented in Chapter Ten, as well as an overview of ecology.

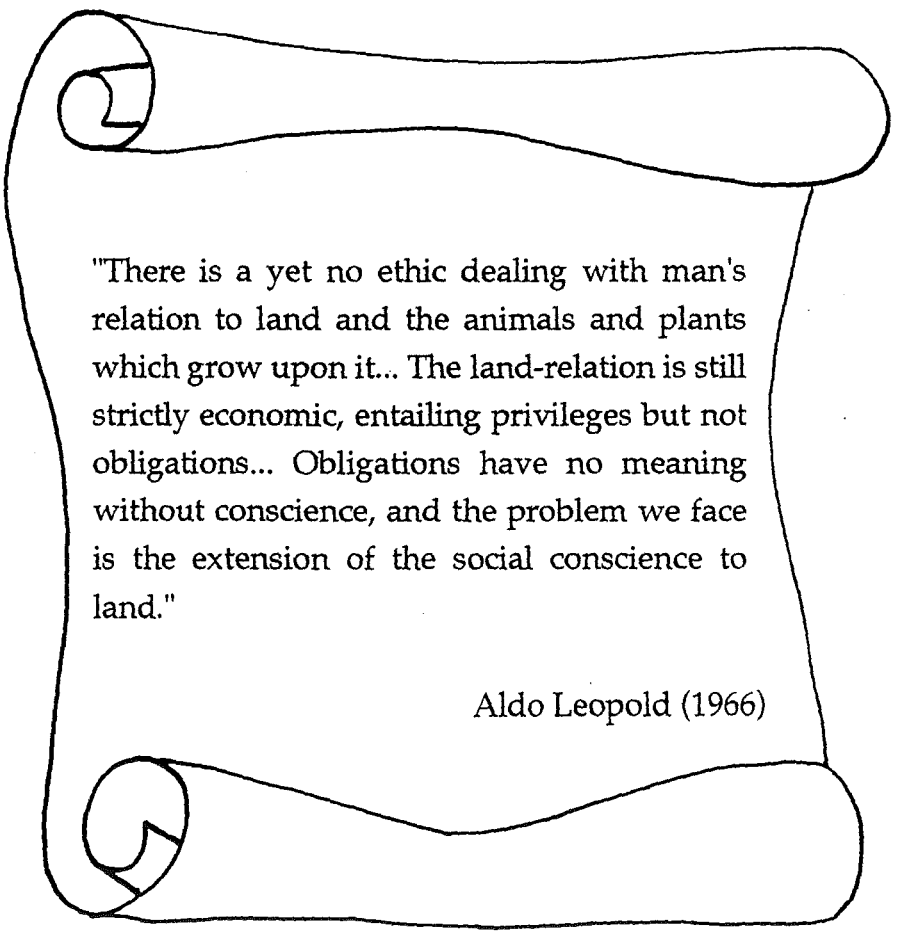
2. To assess the future survival of *Podocarpus totara* in a fragmented landscape

• Determine whether the current floristic composition and structure of totara dominated fragments will be sustained in the future or whether new areas must be provided for regeneration so as to ensure the persistence of lowland totara. The ecology of lowland totara dictates that catastrophic disturbance is essential for stand initiation. In the absence of disturbance, areas for the revegetation of lowland totara must be provided for. This is discussed in Chapter Twelve.

• Discuss and review the restoration of *Podocarpus totara* dominated forest, management options, and the long term survival of this species in a fragmented landscape, based on ecological knowledge. A review of the effects of fragmentation is presented in Chapter Eleven. A fragmented region (Banks Peninsula) is studied in more detail, showing remnant distribution, size and shape. Options for management are discussed.

• Produce an example of an integrated landscape management plan to allow for sound land use practices and forest regeneration. This plan is presented in Chapter Twelve. Sustainable land use is advocated as well as remnant management and revegetation of denuded pastoral land. Catchment-based landscape management, lowland forest management, and the new landscape ethic are discussed in Chapter Thirteen.

Details of publications arising from the current research appear in Appendix Five.



"There is a yet no ethic dealing with man's relation to land and the animals and plants which grow upon it... The land-relation is still strictly economic, entailing privileges but not obligations... Obligations have no meaning without conscience, and the problem we face is the extension of the social conscience to land."

Aldo Leopold (1966)

REFERENCES

Allan,H.H. (1961). 'Flora of New Zealand, Volume 1.' Wellington, Government Printer.

Arlidge,M. (1992). 'Phenology, dendrochronology, population structure: The ecology of sex in kahikatea (*Dacrycarpus dacrydioides*). Unpub. Msc thesis, University of Auckland, New Zealand.

Arnold,G.W.; Steven,D.E.; Weeldenburg,J.R.; Smith,E.A. (1993). 'Influences of remnant size, spacing pattern and connectivity in Euros *Macropus robustus* living in a fragmented landscape.' *Biological conservation 64*: 219 - 223

Atkinson,I.A.E. (1988). 'Opportunities for ecological restoration.' *New Zealand Journal of Ecology 11:* 1 - 12

Atkinson,I. (1989). 'Introduced animals and extinctions.' pp 54- In D.Western & M.C.Pearl (eds). 'Conservation for the twentyfirst century.' Oxford Uni Press, New York.

Atkinson,I.A.E.; Greenwood,R.M. (1972). 'Effects of the 1969-70 drought on two remnants of indigenous lowland forest in the Manawatu district.' *Proceedings of the New Zealand Ecological Society 19*: 34 - 42

Banks Peninsula District Council. (1997). 'Proposed district plan.' Banks Peninsula District Council. 404p

Bathgate,J.L. (1981). 'Holloway's climatic change hypothesis. A quantitative evaluation in the Longwood forests.' Unpublished PhD thesis. University of Canterbury, Christchurch.

Batley,R.A.L. (1956). 'Some practical aspects of dendrochronology in New Zealand.' *Journal of the Polynesian Society 65*: 232 - 244

Battin,J. (1993). 'The relationship between crown and stem dimensions in differing New Zealand forest types.' Unpublished MSc report, University of Canterbury.

Baylis,G.T.S. (1969). 'Synthesis of mycorrhizas in *Podocarpus* and *Agathis* with endogone spores.' *Nature 221*: 1267 - 1268

Baylis,G.T.S.; McNabb,R.F.R.; Morrison,T.M. (1963). 'The mycorrhizal nodules of podocarps.' *Transactions British Mycological Society 46*: 378 - 384

Bell,R.E. (1958). 'Proceedings of the New Zealand Archaeology Society: 4 - Dendrochronology.' *New Zealand Science Review 16*: 13 - 17

Bell,V.; Bell,R.E. (1958). 'Dendrochronological studies in New Zealand.' *TreeRing Bulletin 22*: 7 - 11

Bellingham, P. (1982). 'Some ecological aspects of matai (*Podocarpus spicatus* R.Br. ex Mirbel) in west Taupo indigenous forests.' Unpublished BFS dissertation, University of Canterbury.

Bergin,D.O.; Ecroyd,C.E. (1987). 'Totara provinance trial - seed collection and measurement.' Unpublished I.F.M.P.R. No. 1751. Rotorua, Forest Research Institute.

Bergin,D.O.; Kimberley,M.O. (1992). 'Provinance variation in *Podocarpus totara*.' *New Zealand Journal of Ecology 16*: 5 - 13

Bergin,D.O.; Pardy,G.F. (1987). 'Growing totara.' *New Zealand Tree Grower August*: 68 - 70

Bergin,D.O.; Pardy,G.F. (1990). 'A survey of established native tree plantings.' *New ZealandTree Grower 11*: 2 - 7

Bergin,D.O.; Pardy,G.F.; Beveridge,T. (1988). 'Planting to restore or extend native forest remnants.' *New Zealand Tree Grower 9*: 44 - 47

Best,E. (1977). 'Forest lore of the Maori.' Wellington, Government Printer.

Beveridge,A.E. (1964). 'Dispersal and destruction of seed in central North Island.' *Proceedings New Zealand Ecological Society 11* : 48 - 55

Beveridge,A.E. (1973a). 'Regeneration of podocarps in a central North Island forest.' *New Zealand Journal of Forestry 18*: 23 - 35

Beveridge,A.E. (1973b). 'Dispersal and destruction of seed in central North Island podocarp forests.' *Proceedings of the New Zealand Ecological Society 4*: 48 - 55

Beveridge,A.E. (1983). 'Regeneration of podocarp forests and the maintenance of productivity.' pp 93 - 112 In K.Thompson, A.P.Hodder, A.S.Edmonds (eds). 'Lowland forests in New Zealand.' Hamilton, University of Waikato.

Beveridge,A.E.; Bergin,D.O.; Pardy,G. (1987). 'Guidelines for planting native trees.' Unpublished I.F.M.P. No. IFM9. Rotorua, Forest Research Institute.

Beveridge,A.E.; Smale,M.C. (1981). 'Seeding of native species.' In C.G.R.Chavasse (ed). 'Forest nursery and establishment practice in New Zealand.' F.R.I. Symposium No.22, Forest Research Institute.

Bierregaard,R.O.Jnr, Dos Santos,A.A.; Hutchings,R.W. (1990). 'Biological dynamics of forest fragments project (M.C.S.E.P.)'. 11th Annual Report. U.S.N.M.N.H. & I.N.P.A.

Bierregaard,R.O.Jnr,; Lovejoy,T.E.; Kapos,V.; Dos Santos,A.; Hutchings,R.W. (1992). 'The biological dynamics of tropical rainforest fragments - a prospective comparison of fragments and continuous forest.' *BioScience* 42(11): 859 - 866

Billington,H.L.; Sweet,G.B. (in prep.). 'Genetic variation in New Zealand podocarps.'

Blaschke,P.M.; Hunter,G.G.; Eyles,G.O.; Van Berkel,P.R. (1981). 'Analysis of New Zealand's vegetation cover using land resource inventory data.' *New Zealand Journal of Ecology 4*: 1 - 19

Bond,G. (1967). 'Fixation of nitrogen by higher plants other than legumes.' *Annual Review of Plant Physiology 18*: 107 - 126

Bradby,K. (1991). 'A data bank is never enough: the local approach to landcare.' pp 377 - 385 In D.A.Saunders; R.J.Hobbs (eds). 'Nature conservation 2: the role of corridors.' Surrey Beatty & Sons, NSW.

Bridgewater,P.B. (1987). 'Connectivity: an Australian perspective.' pp 195 - 200 In D.A.Saunders et al (eds). 'Nature conservation: the role of remnants of native vegetation.' Surrey Beatty & Sons, NSW. 410p

Brooker,S.G.; Cambie,R.C.; Cooper,R.C. (1987). 'New Zealand medicinal plants.' Auckland, Heinemann.

Brooker,S.G.; Cambie,R.C.; Cooper,R.C. (1988). 'Economic native plants of New Zealand.' Christchurch, Botany Division D.S.I.R.

Buchholz,J.T.; Gray,N.E. (1948). 'A taxonomic revision of *Podocarpus* 1. The sections of the genus and their subdivisions with special reference to leaf anatomy.' *Journal of the Arnold Arboretum 29*: 49 - 76

Bull,W.B. (no date). 'New Zealand earthquakes, rockfalls, and lichens - a progress report.' Unpub. report. Geosciences Department, University of Arizona.

Burgess,R.L. & Sharpe,D.M. (1981). 'Forest island dynamics in man-dominated landscapes.' Springer, New York.

Burke,W.D. (1974). 'Regeneration of podocarps on Mt Tarawera, Rotorua.' *New Zealand Journal of Botany 12* : 219 - 226

Burrows,C.J. (1969). 'Forest distribution and the forest shrub flora.' pp 226 - 256 In G.A.Knox (ed). 'The natural history of Canterbury.' Wellington, A.H. & A.W.Reed.

Burrows,C.J. (1995). 'Further germination experiments on the seeds of native plants.' *Canterbury Botanical Society Journal 29.* 69 - 75

Burrows,C.J.; Randall,P.; Moar,N.T.; Butterfield,B.G. (1993). 'Aranuian vegetation history of the Arrowsmith Range, Canterbury, New Zealand. 111. Vegetation changes in the Cameron, upper south Ashburton, and Paddle Hill Creek catchments.' *New Zealand Journal of Botany 31*: 147 - 174

Cambie,R.C. (1976). 'A New Zealand phytochemical register - Part 111.' *Journal of the Royal Society of New Zealand 6*: 307 - 379

Cambie,R.C.; James,M.A. (1967). 'The taxonomic distribution of some biflavonoids.' *New Zealand Journal of Science 10* : 918 - 926

Cambie,R.C.; Simpson,W.R.J.; Colebrook,L.D. (1963). 'Chemistry of the Podocarpaceae - V11. Podototarin and the constituents of the heartwood of *Podocarpus hallii* Kirk..' *Tetrahedron 19*: 209 - 217

Cameron,R.J. (1955). 'Mosaic or cyclical regeneration in North Island podocarp forests.' *New Zealand Journal of Forestry 7*: 55 - 64

Cameron,R.J. (1960a). 'Natural regeneration of podocarps in the forests of the Whirinaki River Valley.' *New Zealand Journal of Forestry 8* : 337 - 354

Cameron,R.J. (1960b). 'Dendrochronology in New Zealand.' *Journal of the Polynesian Society 69*: 37 - 38

Campbell,I.B. (1973). 'Pattern of variation in steepland soils: variation on a single slope.' *New Zealand Journal of Science 16*: 413 - 434

Campbell,I.B. (1975). 'Pattern of variation in steepland soils: soil differences in complex topography.' *New Zealand Journal of Science 18*: 53 - 66

Carroll,C.R. (1991). 'Interface between natural areas and agroecosystems.' pp 365 - 384 In C.R.Carroll et al (eds). 'Agroecology.' McGraw-Hill, New York.

Clark,R. (1993). 'Lusitanica promising tree for the Peninsula'. Christchurch Star, April 13th, page 8.

Clifton,N.C. (1990). 'New Zealand timbers.' Wellington, Government Printer Books.

Clout,M.N.; Hay,J.R. (1989). 'The importance of birds as browsers, pollinators and seed dispersers in New Zealand forest.' *New Zealand Journal of Ecology 12 (supp.)*: 27 - 34

Cockayne,L. (1923). 'Hybridism in the New Zealand flora.' *New Phytologist* 22: 105 - 127

Cockayne,L. (1928). 'The vegetation of New Zealand.' 2nd edition. Liepzig, Englemann.

Cockayne,L. (1932). 'Polymorphy in New Zealand conifers and its relation to horticulture.' pp 151 - 164 In F.J.Chittenden (ed) 'Conifers in cultivation.' London, Royal Horticultural Society.

Cockayne,L.; Allan,H.H. (1934). 'An annotated list of groups of wild hybrids in the New Zealand flora.' *Annals of Botany 48*: 1 - 55

Cockayne,L.; Phillips Turner,E. (1939). 'The trees of New Zealand.' Wellington, Government Printer.

Connor,H.E.; Edgar,E. (1987). 'Name changes in the indigenous New Zealand flora, 1960 - 1986 and Nomina Nova 1V, 1983 - 1986.' *New Zealand Journal of Botany 25*: 115 - 170

Cooper,R.C.; Cambie,R.C. (1991). 'New Zealand's economic native plants.' Auckland, Oxford University Press.

Cornere,B.M. (1992). 'Population dynamics of a lowland terrace rimu forest, south Westland, New Zealand.' Unpub. MForSc, University of Canterbury, NZ.

Cornere,B.M.; Norton,D.A. (in prep.). 'Spatial pattern of stand structure in a lowland New Zealand podocarp forest.'

Couper,D. (1993). 'What information to primary producers need from ecologists?.' pp 215 - 223 In D.A.Saunders et al (eds). Nature conservation 3: Reconstruction of fragmented ecosystems.' Surrey Beatty & Sons.

Couper,R.A. (1953). 'Distribution of *Protaceae, Fagaceae,* and *Podocarpaceae* in some southern hemisphere cretaceous and tertiary beds. '*New Zealand Journal of Science and Technology Series B 35*: 247 - 250

Cranwell,L.M. (1940). 'Pollen grains of the New Zealand conifers.' *New Zealand Journal of Science and Technology Series B* 22: 1 - 17

Crowe,A. (1990). 'Native edible plants of New Zealand.' Auckland, Hodder & Stoughton.

Cunningham,G.H. (1963). 'The Thelephoraceae of Australia and New Zealand.' Bulletin 145, New Zealand D.S.I.R.

Cunningham,G.H. (1965). 'Polyporaceae of New Zealand.' Bulletin 164, New Zealand D.S.I.R.

Dawkins,H.C. (1963). 'Crown diameters: thier relation to bole diameter in tropical forest trees.' *Commonwealth Forestry Review 42*: 318 - 333

DeLaubenfels,D.J. (1969). 'A revision of the Malesian and Pacific rainforest conifers, 1. Podocarpaceae. Parts 1 & 2.' *Journal of the Arnold Arboretum 50*: 274 - 369

Diamond,J.M. (1975). 'The island dilemma: lessons for modern biogeographic studies for the design of nature reserves.' *Biological conservation* 7: 129 - 146

Diamond,J.M. (1978). 'Critical areas for maintaining viable populations of species.' pp 27 - 37 In M.W.Holgate; M.J.Woodman (eds). 'The breakdown and restoration of ecosystems.' Plenium Press, New York

Diamond,J.M. (1984). ' "Normal" extinctions in isolated populations.' pp 191 - 246 In M.H.Nitecki (ed). 'Extinctions.' Uni of Chicago Press, Chicago.

Diggle,P.J. (1983). 'Statistical analysis of spatial point patterns.' Academic Press, London.

Druce,A.P. (1966). 'Secondary totara-titoki-matai forest on the Otaki Plain.' *Bulletin Wellington Botanical Society 33*: 22 - 39

Druguid,F.C.; Druce,A.P. (1966). 'Totara forest at Ohau.' *Bulletin Wellington Botanical Society 33*: 20 - 21

Duncan,R.P. (1989). 'An evaluation of errors in tree age estimates based on increment cores in kahikatea (*Dacrycarpus dacrydioides*).' *New Zealand Natural Sciences 16* : 31 - 37

Duncan,R.P. (1991). 'Disturbance, succession, and the coexistence of species in a lowland podocarp forest, south Westland, New Zealand.' Unpub. PhD thesis, University of Canterbury, NZ.

Duncan,R.P.; Stewart,G.H. (1991). 'The temporal and spatial analysis of tree age distributions.' *Canadian Journal of Forest Research 21*:

Duncan,R.P. (1993) 'Flood disturbance and the coexistance of species in a lowland podocarp forest, south Westland, New Zealand.' *Journal of Ecology 81*: 403 - 416

Dunwiddie,P.W. (1979). 'Dendrochronological studies of indigenous New Zealand trees.' *New Zealand Journal of Botany 17*: 251 - 266

Ebbett,R.L. (1992). 'Ecological charactorization of dense lowland podocarp forest, Whirinaki Sanctuary.' Unpublished MEnvSc thesis. University of Auckland, Auckland.

Ebbett,R.L.; Norton,D.A. (in prep). 'The ecology of endemic Podocarpus: a review.'

Ebbett,R.L.; Ogden,J. (1998). 'Seedling growth of five endemic New Zealand podocarp species under different light regimes.' *New Zealand Journal of Botany* 36 (2)

Edgar,E.; Connor,H.E. (1983). 'Nomina Nova 111, 1977-1982.' *New Zealand Journal of Botany 21*: 421 - 441

Ehrlich,A.H. (1993). 'Monitoring populations on remnants of native vegetation.' pp 201 - 210 In D.A.Saunders et al (eds) 'Nature conservation: the role of remnants of native vegetation.' Surrey Beatty & Sons, NSW.

Ehrlich,P.R.; Murphy,D.D. (1987). 'Global co-operation and ecosystem restoration.' pp 17 - 25 In D.A.Saunders et al (eds) 'Nature conservation 3: reconstruction of fragmented ecosystems' Surrey Beatty & Sons, NSW.

Esler,A.E. (1978). 'Botany of the Manawatu district, New Zealand.' Wellington, Government Printer.

Evans,B. (1983). 'Revegetation manual; a guide to revegetation using New Zealand native plants.' QE11 Natioanl trust, Wellington.

Fahrig,L.; Merriam,G. (1985). 'Habitat patch connectivity and population survival.' *Ecology* 66(6): 1762 - 1768

Farjon,A.; Page,C.N.; Schellevis,N. (1993). 'A preliminary world list of threatened conifer taxa.' *Biodiversity and Conservation 2*: 304 - 326

Farr,W.A.; DeMars,D.J.; Dealy,J.E. (1989). 'Height and crown width related to diameter for open-grown western hemlock and Sitka spruce.' *Canadian Journal of Forest Research 19:* 1203 - 1207

Fleming,C.A. (1975). 'The geological history of New Zealand and its biota.' pp 1 - 86 In G.Kushel (ed) 'Biogeography and ecology in New Zealand.'

Forest Research Institute. (1980). 'Raising native trees.' *What's new in forest research No. 85.* Rotorua, Forest Research Institute.

Forest Research Institute. (1989). 'Growth of native trees in plantations.' *What's new in forest research No. 173.* Rotorua, Forest Research Institute.

Forman,R.T.; Godron,M. (1986). 'Landscape ecology.' John Wiley & Sons, New York. 619p

Fountain,D.W.; Outred,H.A. (1991). 'Germination requirements of New Zealand native plants: a review.' *New Zealand Journal of Botany 29:* 311 - 316

Foweraker,C.E. (1929). 'The podocarp rain forests of Westland, New Zealand.' *Te Kura Ngahere* 2: 6 - 12

Franklin,D.A. (1968). 'Biological flora of New Zealand. 3. *Dacrydium cupressinum* Lamb. (Podocarpaceae) rimu.' *New Zealand Journal of Botany 6*: 493 - 513

Franklin,D.A. (1973). "Growth rates in south Westland terrace rimu forest. 1. Growing stock and increment in virgin forest.' *New Zealand Journal of Forestry Science 3*: 304 - 312

Fritts,H.C. (1976). 'Tree rings and climate.' Academic press, London.

Gardner,R.O. (1990). 'Totara and Hall's totara.' *Auckland Botanical Society Journal 45* : 27 - 28

Garwood,N.C.; Janos,D.P.; Brokaw,N. (1979). 'Earthquake-caused landslides: a major disturbance to tropical forests.' *Science 205* : 997 - 999

Gerard,A.J. (1981). 'Soils and landforms. An integration of geomorphology and pedology.' George Allen and Unwin, London. 219pp

Gibbs,H.S. (1980a). 'Development and plant relationships of lowland forest soils.' pp 35 - 44 In K.Thompson et al (eds). 'Lowland forests in New Zealand.' Centre for Continuing Education and Environmental Studies Unit, Massey University.

Gibbs,H.S. (1980b). "New Zealand soils; an introduction." Oxford University press, Wellington. 117p

Gilpin,M.E.; Soule',M.E. (1986). 'Minimum viable populations: processes of species extinctions.' pp 19 - 34 In M.E.Soule' (ed). 'Conservation biology: the science of scarcity and diversity.' Sinauer.

Godley,E.J. (1975). 'Flora and vegetation.' pp 177 - 229 In G.Kushel (ed) 'Biogeography and ecology in New Zealand.'

Godron,M.; Forman,R.T.T. (1983). 'Landscape modification and changing ecological charactoristics.' pp 12 - 28 In H.A.Mooney & M. Godron (eds). 'Disturbance and ecosystems.' Springer-Verlag, Berlin

Gordon,M. (1944). 'The garden of Tane.' Wellington, A.H. & A.W.Reed.

Great Britain D.S.I.R. (1945). 'A handbook of empire timbers.' London, His Majesty's Stationery Office.

Green,D.R.; Cummins,R.: Wright,R.; Miles,J. (1993). A methodology for aquiring information on vegetation succession from remotely sensed imagery.' p 111 - 129 *In* R.Haines-Young et al (eds). 'Landscape ecology and geographic information systems.' Taylor & Francis London.

Greenwood,R.M. (1949). 'Totara reserve. '*Bulletin Wellington Botanical Society 21*: 2 - 7

Griffin,E.M. (1907). 'The development of some New Zealand conifer leaves with regard to transfusion tissue and its adaptation to environment.' *Transactions and Proceedings of the New Zealand Institute 15*: 43 - 72

Hall,R.J. (1993). 'An approach to natural hazard assessments and hazard reduction.' Unpub. PhD thesis, Lincoln University, New Zealand.

Hansson,L.; Fahrig,L.; Merriam,G. eds (1995). 'Mosaic landscapes and ecological processes'. Chapman & Hall, London. 356p

Harris,L.D. (1984). 'The fragmented forest: island biogeographic theory and the preservation of biotic diversity.' Uni of Chicago Press, Chic.

Harris,L.D.; Silva-Lopez,G. (1992). 'Forest fragmentation and the conservation of biological diversity.' pp 197 - 237 In P.L.Fiedler & S.K.Jain (eds). 'Conservation biology.' Chapman & Hall, New York.

Hawkins,B.J. (1988). 'Investigations of the physiology and genetics of the New Zealand conifers: rimu, kahikatea and totara.' Unpublished PhD thesis. University of Canterbury, Christchurch.

Hawkins,B.J.; Sweet,G.B. (1989a). 'Evolutionary interpretation of a high temperature growth response in five New Zealand forest tree species.' *New Zealand Journal of Botany 27*:: 101 - 107

Hawkins,B.J.; Sweet,G.B. (1989b). 'The growth of three podocarp species under different nutrient regimes.' *New Zealand Journal of Botany 29*: 455 - 458

Hawkins,B.J.; Sweet,G.B.; Greer,D.H.; Bergin,D.O. (1991). 'Genetic variation in the frost hardiness of *Podocarpus totara*.' *New Zealand Journal of Botany 29* : 455 - 458

Herbert,J. (1976). 'Raising seedlings from seed contained in forest duff.' Unpublished Indigenous Silvicultural Report No. 15. Rotorua, New Zealand Forest Service.

Herbert,J. (1980). 'Structure and growth of dense podocarp forest at Tihoi, Central North Island, and the impact of selective logging.'*New Zealand Journal of Forestry 25*: 44 - 57

Higgs,A.J.; Usher,M.B. (1980). 'Should nature reserves be large or small?.' *Nature* 285: 568

Hill,D.B. (1985). 'Forest fragmentation and its implications in central New York.' *Forest Ecology & Mangement 12*: 113 - 128

Hinds,H.V.; Reed,J.S. (1957). 'Forest trees and timbers of New Zealand.' N.Z.F.S. Bulletin No.12. Wellington, Government Printer.

Hobbs,R.J. (1987). 'Disturbance regimes in remnants of natural vegetation.' pp 233 - 240 In D.A.Saunders et al (eds). 'Nature Conservation: the role of remnants of native vegetation.' Surrey Beatty & Sons, NSW.

Hobbs,R.J. (1993). 'Effects of landscape fragmentation on ecosystem processes in the Western Australian wheatbelt.' *Biol ogicalConservation* 64: 193 - 201

Hobbs,R.J.; Saunders,D.A. eds (1993). 'Reintegrating fragmented landscapes.' Springer-Verlag, New York.

Hobbs,R.J., Saunders,D.A., Lobby De Bruyn,L.A.; Main,A.R. (1993a). 'Changes in biota.' pp 65 - 106 In R.J.Hobbs; D.A.Saunders (eds). 'Reintegrating fragmented landscapes.' Springer-Verlag, NY.

Hobbs,R.J. Saunders,D.A.; Main,A.R. (1993b). 'Conservation management in fragmented systems.' pp 279 - 296 In R.J.Hobbs; D.A.Saunders (eds). 'Reintegrating fragmented landscapes.' Springer-Verlag, New York.

Holdgate,M.W.; Woodman,M.J. eds (1978). 'The breakdown and restoration of ecosystems.' Plenium Press, New York.

Holloway,J.T. (1954). 'Forests and climate in the South Island of New Zealand.' *Transactions of the Royal Society of New Zealand 82*: 329 - 410

Hopkins,A.J.M.; Saunders,D.A. (1987). 'Ecological studies as the basis for management.' pp 15 - 28 In D.A.Saunders et al (eds).'Nature conservation: the role of remnants of native vegetation.' Surrey Beatty & Sons, NSW.

Hora,B. ed (1980). 'The Oxford encyclopedia of trees of the world.' Oxford, Peerage Books.

Innes,K.P.C.; Kelly,D. (1992). 'Water potentials in native woody vegetation during and after a drought in Canterbury.' *New Zealand Journal of Botany 30*: 81 - 94

James,I.L.; Griffiths,A.D. (no date). 'Early planting trials of rimu, Kahikatea and totara in South Westland.' Unpublished I.F.M.P.R. No.FRI44. Rotorua, Forest Research Institute.

Jane,G. (1983). 'The impact of introduced herbivores on lowland forests of the North Island.' pp 135 - 152 In K.Thompson, A.P.Hodder, A.S.Edmonds (eds) 'Lowland forests in New Zealand.' Hamilton, University of Waikato.

Janzen,D.H. (1983). 'No park is an island: increase in interference from outside as park size decreases.' *Oikos* 41: 402 - 410

Johnson,P.N. (1973). 'Mycorrhizas of coniferous - broadleaved forest.' Unpublished PhD thesis. University of Otago, Dunedin.

Johnston,W.B. (1961). 'Locating the vegetation of early Canterbury: a map and the sources.' *Transactions of the Royal Society of New Zealand 1* : 5 - 15

Johnston,W.B. (1969). 'Modification of the natural environment by man.' pp 77 - 94 In G.A.Knox (ed) 'The natural history of Canterbury.' Wellington, A.H. & A.W.Reed.

Kaeiser,M. (1954). 'Microstructure of wood of *Podocarpus*. '*Phytomorphology* 4: 39 - 47

Kapos,V. (1989). 'Effects of isolation on the water status of forest patches in the Brazilian Amazon.' *Journal of Tropical Ecology* 5: 173 - 185

Katz,A. (1980a). 'Growth of podocarp pole stands on former Maori-cleared sites in the Whirinaki River Valley.' Unpublished I.F.M. Report No.24. Forest Research Institute, New Zealand Forest Service.

Katz,A. (1980b). 'Structure and growth of dense podocarp forest in Whirinaki.' Unpublished I.F.M. Report No.25. Forest Research Institute, New Zealand Forest Service.

Kelly,G.C. (1972). 'Scenic Reserves of Canterbury.' Biological Survey of Reserves, Report 2. DSIR, New Zealand.

Kelly,G.C.; Park,G.N. eds (1986). 'The New Zealand protected natural areas programme - a scientific focus.' Technical Advisory Group. NZ Biological Resources Centre Pub. No. 4. Wellington.

Kubricki,A.; Denby,C.; Stevens,M.; Haagensen,A.; Chatfield,J. (1993). 'Determining the long-term costs and benefits of alternative farm plans.' pp 245 - 278 In R.J.Hobbs; D.A.Saunders (eds). 'Reintegrating fragmented landscapes.' Springer-Verlag, New York.

Lapin,L.L. (1975). 'Statistics; meaning and method.' Harcourt Brace Jovanovich, Inc., New York. 591pp

Lavers,C.P.; Haines-Young,R. (1993). 'Equilibrium landscapes and their aftermath: spatial heterogeneity and the role of new technology.' pp 57 - 74 *In* R.Haines-Young et al (eds). 'Landscape ecology and geographic information systems.' Taylor & Francis London.

Leathwick,J.R.; Rogers,G.M. (1996). 'Modelling relationships between environment and canopy composition in secondary vegetation in central North Island, New Zealand.' *New Zealand Journal of Ecology 20(2)*: 147 - 161

Leech,J.W. (1984). 'Estimating crown width from diameter at breast height for open-grown radiata pine trees in South Australia.' *Australian Journal of Forest Research 14:* 333 - 337

Lefroy,E.C.; Hobbs,R.J. (1993). 'Some human responses to global problems.' pp 33 - 39 In D.A.Saunders et al (eds). 'Nature conservation 3: reconstruction of fragmented ecosystems.' Surrey Beatty & Sons, NSW.

Legendre,P.; Fortin,M. (1989). 'Spatial pattern and ecological analysis.' *Vegetatio 80*: 107 - 138

Leopold,A. (1966). 'A Sand County Almanac; with other essays from Round River.' O.U.P., New York.

Levenson,J.B. (1981). 'Woodlots as biogeographic islands in southeastern Wisconsin.' pp 13 - 40 In R.L.Burgess & D.M.Sharpe (eds). 'Forest island dynamics in man-dominated landscapes.' Springer, NY.

Lloyd,R.C. (1960). 'Indigenous tree rings.' *New Zealand Journal of Forestry 8*: 824 - 825

Loh,G. (1981). 'Scenic Reserves of north Westland.' Biological Survey of Reserves Series No. 7. DOSLI, Wellington.

Loney,B.; Hobbs,R.J. (1991). 'Managment of vegetation corridors: maintenance, rehabilitation and establishment.' pp 299 - 311 In D.A.Saunders; R.J.Hobbs (eds). 'Nature conservation 2: the role of corridors.' Surrey Beatty & Sons, NSW.

Lord,J.M.; Norton,D.A. (1990). 'Scale and the spatial concept of fragmentation.' *Conservation Biology* 4(2): 197 - 202

Lorimer,C.G. (1985). 'Methodological considerations in the analysis of forest disturbance history.' *Canadian Journal of Forestry Research 15* : 200 - 213

Lotwick,H.W.; Silverman,B.W. (1983). 'Methods for analysing spatial processes of several types of points.' *Journal of the Royal Statistical Society, Series B 44:* 406 - 413

Lovejoy,T.E.; Oren,D.C. (1981). 'The minimum critical size of ecosystems.' pp 7 - 12 In R.L.Burgess & D.M.Sharpe (eds). 'Forest island dynamics in man-dominated landscapes.' Springer-Verlag, NY.

Lovejoy,T.E., Bierregaard,R.O.Jnr,; RylandsA.B. (1986). 'Edge and other effects of isolation on Amazonian forest fragments.' pp 257 - 285 In M.E.Soule' (ed). 'Conservation biology.' Sinauer.

Lovejoy,T.E., Rankin,J.M., Bierregaard,R.O.Jnr, Brown,K.S., Emmons,L.H.; Van Der Voort,M.E. (1984). 'Ecosystem decay of Amazon forest remnants.' pp 295 - 325 In M.H.Nitecki (ed). 'Extinctions.' Uni of Chicago Press, Chicago.

Loyn,R.H. (1987). 'Effects of patch area and habitat on bird abundances, species numbers and tree health in fragmented Victoria' pp 65 - 77 In D.A.Saunders et al (eds). 'Nature conservation: the role of remnants of native vegetation.' Surrey Beatty & Sons, NSW.

Lucas,D. (1987). 'Woodlots in the landscape.' Landscape Publications Ltd, Wellington. 24p

Lusk,C.H. (1989). 'Age structure and dynamics of podocarp-broadleaved forest in Tongariro National Park.' Unpublished PhD thesis. University of Auckland, Auckland.

Lusk,C.H.; Ogden,J. (1992). 'Age structure and dynamics of a podocarp-broadleaf forest in Tongariro National Park, New Zealand.' *Journal of Ecology 80*: 379 - 393

MacArthur,R.H.; Wilson,E.O. (1967). 'The theory of island biogeography.' Princeton University Press, New Jersey.

Main, A.R. (1987). 'Management of remnants of native vegetation - a review of the problems and the development of an approach with reference to the wheatbelt of Western Australia.' pp 1 - 13 In D.A.Saunders et al (eds). ' Nature conservation: the role of remnants of native vegetation.' Surrey Beatty & Sons, NSW.

Margules,S.C.; Higgs,A.J.; Rafe,R.W. (1982). 'Modern biogeographic theory: are there any lessons for nature reserve design?.' *Biological Conservation 24*: 115 - 128

Markham,K.R.; Webby,R.F.; Whitehouse,L.A.; Molloy,B.P.J.; Vilain,C.; Mues,R. (1985). 'Support from flavonoid glycoside distribution for the division of *Podocarpus* in New Zealand.' *New Zealand Journal of Botany 23*: 1 - 13

Massam,D.G. (1986). 'After the flood - a study of management problems directly arising from the flash flood which occurred on the Mt. Peel Range January 1975.' Unpub. Dissertation, Lincoln College, New Zealand.

McEwen,W.M. (1978). 'The food of the New Zealand pigeon (*Hemiphaga novaeseelandiae novaeseelandiae*).' *New Zealand Journal of Ecology 1*: 99 - 108

McEwen,W.M. (1988). 'Cone and seed phenology in several New Zealand conifer tree species.' *Tuatara 30*: 66 - 76

McGlone,M.S. (1983a). 'History of New Zealand lowland forest since the last glaciation.' pp 1 - 17 In K.Thompson, A.P.Hodder, A.S.Edmonds (eds) 'Lowland forests in New Zealand.' Hamilton, University of Waikato.

McGlone,M.S. (1983b). 'Polynesian deforestation of New Zealand: a preliminary synthesis.' *Archeaology in Oceania 18*: 11 - 25

McGlone,M.S. (1988). 'New Zealand.' pp 557 - 600 In B.Huntley, T.Webb 11 (eds) 'Vegetation history.' Kluwer Academic Publishers.

McGlone,M.S.; Topping,W.W. (1977). 'Aranuian (post-glacial) pollen diagrams from the Tongariro region, North Island, New Zealand.' *New Zealand Journal of Botany 15*: 749 - 760

McKelvey,P.J. (1963). 'The synecology of the West Taupo indigenous forest.' Wellington, Government Printer.

McKelvey,P.J. (1973). 'The pattern of the Urewera forests.' Technical Paper No.59. Wellington, New Zealand Forest Service.

McKelvey,P.J. (1984). 'Provisional classification of South Island virgin indigenous forests.' *New Zealand Journal of Forestry Science 14*: 151 - 178

McQueen,D.R. (1961). 'Indigenous-induced vegetation and *Pinus radiata* on volcanic ash soils.' *Proceedings of the New Zealand Ecological Society 8*: 1 - 14

McSweeney,G.D. (1982). 'Matai/totara flood plain forests in south Westland.' *New Zealand Journal of Ecology 5*: 121 - 128

Metcalf,L.J. (1991). 'The cultivation of New Zealand trees and shrubs.' Wellington, Reed.

Metson,A.J. (1974). 'The soil we live on (1).' *New Zealands Nature Heritage 1(9)*: 229 - 338

Meylan,B.A.; Butterfield,B.G. (1978). 'The structure of New Zealand woods.' Bulletin 222. Wellington, D.S.I.R.

Mildenhall,D.C. (1980). 'New Zealand late cretaceous and cenozoic plant biogeography: a contribution.' *Paleogeography Paleoclimatology Paleoecology 31*: 197 - 233

Millar,R.I.; Harris,L.D. (1977). 'Isolation and extirpations in wildlife reserves.' *Biological Conservation* 12: 311 - 315

Millett,J. (1987). 'Totaras on the farm.' *New Zealand tree Grower* February: 14 - 15

Ministry of Works and Development (1975). 'New Zealand Land Resource Inventory Worksheet, sheet s94 Akaroa.' 1:63360. Water and Soil Division, New Zealand.

Ministry for the Environment. (1996). 'Sustainable land management; a strategy for New Zealand.' Ministry for the Environment, New Zealand. 16p

Moar,N.T. (1971). 'Contributions to the quaternary history of the New Zealand flora. 6. Aranuian pollen diagrams from Canterbury, Nelson, and north Westland, South Island.' *New Zealand Journal of Botany 9*: 80 - 145

Moar,N.T. (1980). 'Late otiran and early aranuian grassland in central South Island.' *New Zealand Journal of Ecology 3*: 4 - 12

Molesworth,B.E.G. (no date). 'Some growth notes of native trees.' *Auckland Botanical Society Journal 5*: 6 - 8

Mollison,B. (1992). 'Permaculture: a designers' manual.' Tagari Publications, Australia.

Molloy,B.P.J. (1969). 'Recent history of the vegetation.' pp 340 - 360 In G.A.Knox (ed) 'The natural history of Canterbury.' Wellington, A.H. & A.W.Reed.

Molloy,B.P.J.; Burrows,C.J.; Cox,J.E.; Johnston,J.A.; Wardle,P. (1963). 'Distribution of subfossil forest remains, eastern South Island, New Zealand.' *New Zealand Journal of Botany 1*: 68 - 77

Molloy,L. (1988). 'Soils in the New Zealand landscape - the living mantle.' Mallinson Rendel, Wellington. 239p.

Mooney,H.A.; Godron,M. eds (1983). 'Disturbance and ecosystems -components of response.' Springer-Verlag, Berlin. 292p

Moran,P.A.P. (1950). 'Notes on continuous stochastic phenomena.' *Biometrika 37* : 17 - 23

Morton,J.; Ogden,J.; Hughes,T. (1984). 'To save a forest - Whirinaki.' Auckland, David Bateman Ltd.

National Conservation Week Campaign Committee. (1976). 'Growing native seed and seedlings.' Activity Leaflet No.16. Wellington, N.C.W.C.C.

Newsome,P.F.J. (1987). 'The vegetative cover of New Zealand.' Water & Soil Miscellaneous Publication No.112. Wellington, Ministry of Works and Development.

New Zealand Meteorological Service. (1983). 'Summaries of climatological observations to 1980.' NZMS Miscellaneous Publication 177, New Zealand.

New Zealand Meteorological Service. (no date). 'Mean average annual rainfall (mm) 1941-1970.' NZMS 19, 1:500,000.

Nicholls,J.L. (1976). 'A revised classification of the North Island indigenous forests.' *New Zealand Journal of Forestry 21*: 105 - 132

Nicholls,J.L. (1980). 'The past and present extent of New Zealand's indigenous forests.' *Environmental Conservation 7*: 309 - 310

Nicholls,J.L.; Herbert,J.W. (1986). 'A condensed classification of the native forests of New Zealand.' pp 4 - 6 In H.Levack (ed) 'Forestry handbook.' Wellington, New Zealand Institute of Foresters.

Nicholson,G. (1984). 'Methods of soil, plant, and water analysis.' FRI Bulletin No. 70. Forest Research Institute, Rotorua.

Nitecki,M.H. (1984). 'Extinctions.' University of Chicago Press, Chicago.

Norton,D.A. (1988). 'Managing for the long-term.' *Forest and Bird 19(2)* : 32 - 34

Norton,D.A. (1989). 'Management of New Zealand's protected natural areas into the 21st century.' pp 3 - 7 In D.A.Norton (ed). 'Management of New Zealand's natural estate.' New Zealand Ecological Society Occasional Publication No.1.

Norton,D.A. (1991). 'Seedling and sapling distribution patterns in a coastal podocarp forest, Hokitika Ecological District, New Zealand.' *New Zealand Journal of Botany 29* : 463 - 466

Norton,D.A. (1992). 'School of Forestry totara/matai restoration project.' Unpublished report.

Norton,D.A. (1994). 'Relationships between pteridophytes and topography in a lowland South Westland podocarp forest.' *New Zealand Journal of Botany* 32: 401 - 408

Norton,D.A. (1996). 'Development and forest sustainability, Otatara, Invercargill.' Unpublished report for Earnest New & Associates Ltd. Te Wai Pounamu Conservation, Christchurch.

Norton,D.A.; Herbert,J.W.; Beveridge,A.E. (1988). 'The ecology of *Dacrydium cupressinum*: a review.' *New Zealand Journal of Botany 26*: 37 - 62

Norton,D.A.; Ogden,J. (1987). 'Dendrochronology: a review with emphasis on New Zealand applications.' *New Zealand Journal of Ecology 10*: 77 - 95

Norton,D.A.; Palmer,J.G.; Ogden,J. (1987). 'Dendroecological studies in New Zealand. 1. An evaluation of tree age estimates based on increment cores.'*New Zealand Journal of Botany 25*: 373 - 383

Ogden,J. (1985). 'An introduction to plant demography with special reference to New Zealand trees.' *New Zealand Journal of Botany* 23: 751 - 772

Ogden,J. (1995). 'The long-term conservation of forest diversity in New Zealand.' *Pacific Conservation Biology* 2: 77 - 90

Ogden,J. Stewart,G.H. (1995). 'Community dynamics of the New Zealand conifers.' pp 81 - 119 In N.Enright, R.Hill (eds) 'Evolution and ecology of the Southern Hemisphere conifers.' Melbourne University Press & Australian Systematic Society, Australia.

Ogilvie,G. (1992). 'Picturing the Peninsula - early days on Banks Peninsula.' Hazard Press, Christchurch.

Ogle,C.C. (1987). 'The incidence and conservation of animal and plant species in remnants of native vegetation within New Zealand.' pp 79 - 87 In D.A.Saunders et al (eds). 'Nature conservation: the role of remnants of native vegetation.' Surrey Beatty & Sons, NSW.

Palik,B.J.; Murphy,P.G. (1990). 'Disturbance versus edge effects in sugar-maple/beech forest fragments.' *Forest Ecology & Management 32*: 187 - 202

Pardy,G. (1983a). 'Performance of podocarp seedlings planted in reverted cutover forest, S.F.3. Part 3 - Planting in tractor cleared gaps.' Unpublished Production Forestry Division P.R. 255-1. Rotorua, Forest Research Institute.

Pardy,G. (1983b). 'Performance of podocarp seedlings planted in reverted cutover forest, S.F.3. Part - Totara planted in hand cleared gaps.' Unpublished I.F.M. Project No.9. Rotorua, Forest Research Institute.

Park,G.N. (1980). 'The patterns, diversity and conservation status of New Zealand's lowland forests.' In K.Thompson *et al* (eds) 'Lowland forests in New Zealand.' Centre for Continuing Education and Environmental Studies Unit, Massey University.

Park,G.N.; Walls,G.Y. (1978). 'Inventory of tall forest stands on lowland plains and terraces in Nelson and Marlborough land districts, New Zealand.' Botany Division, D.S.I.R.

Patel,R.N. (1967). 'Wood anatomy of Podocarpaceae indigenous to New Zealand. 2. *Podocarpus*. '*New Zealand Journal of Botany 5*: 307 - 321

Pekelharing,C.J.; Batcheler,C.L. (1990). 'The effect of control of brushtail possums (*Trichosurus vulpecula*) on condition of a southern rata/kamahi (*Metrosideros umbellata / Weinmannia racemosa*) forest canopy in Westland, New Zealand. '*New Zealand Journal of Ecology 13:* 73 - 82

Philipson,W.R.; Molloy,B.P.J. (1990). 'Seedling, shoot, and adult morphology of New Zealand conifers. The genera *Darcycarpus, Podocarpus, Dacrydium,* and *Prumnopitys*.'*New Zealand Journal of Botany 28*: 73 - 84

Phillips,J. (1932). 'Root nodules of *Podocarpus*. '*Ecology 13*: 189 - 195

Pickett,S.T.A.; Thompson,J.N. (1978). 'Patch dynamics and the size of nature reserves.' *Biological Conservation 13*: 27 - 37

Pickett,S.T.A.; White,P.S. (1985). 'The ecology of natural disturbance and patch dynamics.' Academic Press, New York.

Pocknall,D.T. (1981). 'Pollen morphology of the New Zealand species of *Dacrydium* Solander, *Podocarpus* L'Heritier, and *Dacrycarpus* Endlicher (Podocarpaceae).' *New Zealand Journal of Botany 19*: 67 - 95

Pollock,K.M. (1986). 'Plant materials handbook for soil conservation. Volume 3: Native plants.' D.S.I.R. Publishing, Wellington.

Poole,A.L.; Adams,N.M. (1990). 'Trees and shrubs of New Zealand.' Wellington, D.S.I.R. Publishing.

Porteous,T. (1993). 'Native forest restoration; a practical guide for landowners.' QE11 National trust, Wellington.

Powlesland,R.G. (1987). 'The foods, foraging behaviour and habitat use of North Island kokako in Puketi State Forest, Northland.' *New Zealand Journal of Ecology 10:* 117 - 128

Preest,D.C. (1963). 'A note on the dispersal charactoristics of the seed of the New Zealand podocarps and beeches and their biogeographical significance.' pp 415 - 424 In N.Z.F.S. Reprint No.72. Pacific basin biogeography symposium. Bishop Museum Press.

QEII National trust (1987). 'The Banks Peninsula landscape.' QEII National Trust, New Zealand. 31pp

Quinn,J.F.; Hastings,A. (1987). 'Extinction in subdivided habitats.' *Conservation Biology* 1: 198-208

Ranney,J.W.; Bruner,M.C.; Levenson,J.B. (1981). 'The importance of edge in the structure and dynamics of forest islands.' pp 67 - 95 In R.L.Burgess & D.M.Sharpe (eds). 'Forest island dynamics in man-dominated landscapes.' Springer, New York.

Ravine,D.A. (1995). 'Manawatu plains ecological district; survey report for the protected natural areas programme.' New Zealand Protected Natural Areas Programme No.33, Department of Conservation, Wanganui.

Reiners,W.A. (1983). 'Disturbance and basic properties of ecosystem energetics.' pp81-93 In H.A.Mooney & M.Godron (eds). 'Disturbance and ecosystems.' Springer-Verlag, New York.

Ridsdill-Smith,T.J. (1987). 'Measuring and monitoring dynamics of remnants. Types of organisms that should be monitored: why and how?.' pp373-373 In D.A.Saunders et al (eds). 'Nature conservation: the role of remnants of native vegetation.' Surrey Beatty & Sons, NSW

Ripley,B.D. (1977). 'Modelling spatial patterns.' *Journal of the Royal Statistical society, Series B 39*: 172-212

Robbins,R.G. (1962). 'The podocarp-broadleaved forests of New Zealand.' *Transactions of the Royal Society of New Zealand 1*: 33-75

Robertson,H.A.; Hackwell,K.R. (1995). 'Habitat preferences of birds in seral kahikatea *Dacrycarpus dacrydioides* (Podocarpaceae) forest of south Westland, New Zealand.' *Biological Conservation 71*: 275-280

Rogers,H.M. (1995). 'Variation in the effects of disturbance along a soil drainage gradient for a lowland temperate rainforest south Westland New Zealand.' Unpublished PhD thesis, University of Canterbury, Christchurch.

Russell,G.B.; Fenemore,P.G. (1970). 'Insect moulting hormone activity of some New Zealand gymnosperms.' *New Zealand Journal of Science 13* : 61-68

Sakai,A.; Paton,D.M.; Wardle,P. (1979). 'Freezing resistance of temperate and sub-arctic conifers native to the southern hemisphere.' *Low Temperature Science Series B 37*: 107-111

Sakai,A.; Wardle,P. (1978). 'Freezing resistance of New Zealand trees and shubs.' *New Zealand Journal of Ecology 1*: 51-61

Salmon,J.T. (1980). 'The native trees of New Zealand.' New Zealand, Heinemann Reid.

Saunders,A. (1980). 'Wildlife and lowland forests.' In K.Thompson *et al* (eds). 'Lowland forests in New Zealand.' Centre for Continuing Education and Environmental Studies Unit, Massey University.

Saunders,D.A.; Hobbs,R.J. (1991a). 'Nature conservation 2: the role of corridors.' Surrey Beatty & Sons, NSW. 442p

Saunders,D.A.; Hobbs,R.J. (1991b). 'The role of corridors in nature conservation: what do we know and where do we go?.' pp421-427 In D.A.Saunders & R.J.Hobbs (eds). 'Nature conservation 2: the role of corridors.' Surrey Beatty & Sons, NSW.

Saunders,D.A.; Arnold,G.W.; Burbidge,A.; Hopkins,A.J.M. (1987). 'The role of remnants of native vegetation in nature conservation: future directions.' pp 387 - 392 In Saunders,D.A. et al (eds). 'Nature conservation: the role of remnants of native vegetation.' Surrey Beatty & Sons, NSW. 410p

Saunders,D.A.; Hobbs,R.J.; Margules,C.R. (1991). 'Biological consequences of ecosystem fragmentation: a review.'*Conservation Biology* 5(1):18-32

Saxton,W.T. (1930). 'The root nodules of the Podocarpaceae.' *South African Journal of Science 22*: 323-325

Shaffer,M.L. (1981). 'Minimum population sizes for species conservation.' *BioScience* 31(2): 131-134

Shaffer,M.L. (1987). 'Minimum viable populations: coping with uncertainty.' pp69-86 In M.E.Soule' (ed). 'Viable populations for conservation.' Cambridge University Press, England.

Shaw,W.B. (1983): Tropical cyclones: determinants of pattern and structure in New Zealand's indigenous forests. *Pacific Science 37*: 405-414

Simberloff,D.S.; Abele,L.G. (1976). 'Island biogeography andconservation: strategy and limitations.' *Science* 193: 1032

Simberloff,D.S.; Abele,L.G. (1982). 'Refuge design and island biogeographic theory: effects of fragmentation.' *American Naturalist* 120: 41-50

Simberloff,D.S.; Cox,J. (1987). 'Consequences and costs of conservation corridors.' *Conservation Biology* 1: 63-71

Simberloff,D.S. (1988). 'The contribution of population and communitybiology to conservation science.' *Ann Rev Eco & Sys* 19: 473-511

Six Dijstra,H.G.; Mead,D.J.; James,I.L. (1985). 'Stand structure in terrace forests of south Westland and its implications for management. *New Zealand Journal of Forestry Science 15* : 3 - 22

Slui,B. (1988). 'Genetic variation in *Podocarpus totara*.' Unpublished B.For.Sc. dissertation. University of Canterbury, Christchurch.

Smale,M.C.; Kimberley,M.O. (1986). 'Growth of naturally regenerated *Beilschmiedia tawa* and podocarps in unlogged and selectively logged podocarp/tawa forest, pureora.' *New Zealand Journal of Forestry Science* 16(2): 131-141

Smith,S.M.; Allen,R.B.; Daly,B.K. (1985). 'Soil-vegetation relationships on a sequence of sand dunes, Tautuku Beach, South-east Otago, New Zealand.' *Journal of the Royal Society of New Zealand 15(3)*: 295-312

Soule',M.E. (1986). 'Conservation biology: the science of scarcity and diversity.' Sinauer, Massachusetts.

Soule',M.E. (1987). 'Viable populations for conservation.' CambridgeUniversity Press, England.

Soule',M.E. (1989). 'Conservation biology in the twenty first century: summary and outlook.' pp297-303 In D.Western & M.C.Pearl(eds). 'Conservation for the twenty first century.' Oxford Uni Press, NY.

Soule',M.E.; Kohm,K.A. (1989). 'Research priorities for conservation biology.' Island Press, Washington D.C.

Sporne,K.R. (1965). 'The morphology of gymnosperms - the structure and evolution of primitive seed plants.' London, Hutchinson University Library.

Spratt,E,.R. (1912). 'The formation and physiological significance of root nodules in the Podocarpaceae.' *Annals of Botany 26*: 801-814

Stewart,G.H.; Basher,L.R.; Burrows,L.E.; Runkle,J.R.; Hall,G.M.J.; Jackson,R.J. (1993). 'Beech-hardwood forest composition, landforms, and soil relationships, north Westland, New Zealand.' *Vegetatio 106*: 111-125

Stewart,G.H.; Rose,A.B. (1989). 'Conifer regeneration failure in New Zealand: dynamics of *Libocedrus bidwillii* stands.' *Vegetatio 79* : 41 - 49

Thompson,K.; Hodder,A.P.; Edmonds,A.S. eds (1980). 'Lowland forests in New Zealand.' Centre for Continuing Education and Environmental Studies Unit, Massey University.

Timmins,S.; Wassilieff,M. (1984). 'The effects of planting programmes on natural distribution and genetics of native plant species.' *The Landscape April*: 18 - 20

Timmins,S.M.; Williams,P.A. (1987). 'Charactoristics of problem weeds in New Zealand's protected natural areas.' pp241-247 In D.A.Saunders et al (eds). 'Nature conservation: the role of remnants of native vegetation.' Surrey Beatty & Sons, NSW.

Timmins,S.M.; Williams,P.A. (1991). 'Weed numbers in New Zealand's forest and scrub reserves.' : 153-162

Tisdale,S.L.; Nelson,W.L.; Beaton,J.D. (1985). 'Soil fertility and fertilizers.' Macmillan Publishing Company, New York. 754p

Townrow,J.A. (1967). 'On Rissikia and Mataia podocarpaceous conifers from the lower mesozoic of southern lands.' *Proceedings of the Royal Society of Tasmania 101*: 103-136

Upton,G.J.G.; Fingleton,B. (1985). 'Spatial data analysis by example.' Volume 1: Point pattern and quantitative data. Wiley, London. 410p.

Usher,M.B. (1987). 'Effects of fragmentation on communities and populations: a review with applications to wildlife conservation.' pp103-121In D.A.Saunders et al (eds). 'Nature conservation: the role of remnants of native vegetation.' Surrey Beatty & Sons, NSW.

Van Berkel,P. ed. (1984). 'The South Island land use capability extended legend for the New Zealand land resource inventory.' National Water and Soil Conservation Organisation. 229p

Veblen,T.T. (1992). 'Regeneration dynamics.' pp153-187 In D.C.Glenn-Lewin et al (eds). 'Plant succession; theory and prediction.' Chapman & Hall, London.

Veblen,T.T.; Stewart,G.H. (1980). 'Comparison of forest structure and regeneration on Bench and Stewart Islands, New Zealand.' *New Zealand Journal of Ecology* 3: 50 - 68

Veblen,T.T.; Stewart,G.H. (1982). 'On the conifer regeneration gap in New Zealand: the dynamics of *Libocedrus bidwillii* stands on South Island.' *Journal of Ecology* 70: 413 - 436

Wairewa County Council. (no date). 'Second Operative District Scheme.' Royds Garden Ltd, Christchurch.

Walker,B. (1989). 'Diversity and stability in ecosystem conservation.'pp 121 - 130 In D.Western & M.C.Pearl (eds). 'Conservation for the twenty first century.' Oxford University Press, New York.

Wardle,P. (1963). 'Growth habits of New Zealand subalpine shrubs and trees.' *New Zealand Journal of Botany 1*: 18-47

Wardle,P. (1972). '*Podocarpus totara* var. *waihoensis* var. nov.: the result of introgressive hybridisation between *P.totara* and *P.acutifolius*.' *New Zealand Journal of Botany 10*: 195-201

Wardle,P. (1974). 'The kahikatea (*Dacrycarpus dacrydioides*) forest of south Westland.' *Proceedings of the New Zealand Ecological Society 21*: 62-71

Wardle,P. (1977). 'Plant communities of Westland National Park (New Zealand) and neighbouring lowland and coastal areas.' *New Zealand Journal of Botany 15*: 323-398

Wardle,P. (1978). 'Regeneration status of some New Zealand conifers, with particular reference to *Libocedrus bidwillii* in Westland National Park.' *New Zealand Journal of Botany 16*: 471-477

Wardle,P. (1985). 'Environmental influences on the vegetation of New Zealand.' *New Zealand Journal of Botany* 23: 773-788

Wardle,P. (1991). 'Vegetation of New Zealand.' Cambridge, Cambridge University Press.

Wardle,P.; Bulfin,M.J.A.; Dugdale,J. (1983). 'Temperate broadleaved evergreen forests of New Zealand.' In J.D.Ovington (ed) 'Temperate broad-leaved evergreen forests.' Amsterdam, Elsevier Science Publishers. Pp 33-71

Wearing,A. (1995). 'Current and prospective distributions of Hall's totara and other forest trees in the pastoral landscapes of Central Otago.' Unpublished Programme and Abstracts, New Zealand Ecological Society 1995 Conference, Massey University.

Webby,R.F.; Markham,K.R.; Molloy,B.P.J. (1987). 'The charactorisation of New Zealand *Podocarpus* hybrids using flavonoid markers.' *New Zealand Journal of Botany 25*: 355-366

Wells,J.A. (1968). 'The ecology of *Podocarpus hallii* in central Otago, New Zealand.' Unpublished PhD thesis. University of Otago, Dunedin.

Wells,J.A. (1972). 'Ecology of *Podocarpus hallii* in Central Otago, New Zealand.' *New Zealand Journal of Botany 10*: 399-426

Wilcove,D.S. (1987). 'From fragmentation to extinction.' *Natural Areas Journal* 7(1):23-29

Williams,P.A. (1982). 'Scenic Reserves of southern Marlborough land district.' Biological Survey of Reserves Series No. 9. DOSLI, Wellington.

Wilson,H.D. (1992). 'Banks ecological region. Port Hills, Herbert and Akaroa ecological districts.' P.N.A. Programme Survey Report No.21. Department of Conservation.

Wilson,H.D. (1994). 'Regeneration of native forest on Hinewai Reserve, Banks Peninsula.' *New Zealand Journal of Botany 32*: 373 - 383

Yeates,J.S. (1924). 'The root-nodules of New Zealand pines.' *New Zealand Journal of Science and Technology 7*: 121-123

Young,A.G. (1988). 'The ecological significance of the 'edge effect' in a fragmented forest landscape.' Unpub MSc thesis, University of Auckland. NZ.

Zimmerman,B.L.; Bierregaard,R.O. (1986). 'Relevence of the equilibrium theory of island biogeography and species area relations to conservation with a case from Amazonia.' *Journal of Biogeography* 13:133-143

APPENDIX ONE
SPECIES LIST AND HERBARIUM SPECIMENS

BOTANICAL NAME	COMMON NAME	MAORI NAME
GYMNOSPERMS		
Dacrycarpus dacrydioides	white pine	kahikatea
Dacrydium cupressinum	red pine	rimu
Podocarpus hallii	Hall's totara	
Podocarpus totara		totara
Prumnopitys ferruginea		miro
Prumnopitys taxifolia	black pine	matai
ANGIOSPERMS		
Alectryon excelsus		titoki
Aristotelia serrata	wineberry	makomako
Ascarina lucida		hutu
Carpodetus serratus	marbleleaf	putaputaweta
Coprosma areolata		
Coprosma grandiflora		
Coprosma rotundifolia		
Dodonea viscosa		akeake
Elaeocarpus dentatus		hinau
Elaeocarpus hookerianus		pokaka
Fuchsia excorticata	tree fuchsia	kotokutuku
Griselinia littoralis	broadleaf	kapuka
Griselinia lucida		puka
Hedycarya arborea	pigeonwood	porokaiwhiri
Hoheria angustifolia	lacebark	
Knightia excelsa	honeysuckle	rewarewa
Kunzea ericoides	tea tree	kanuka
Macropiper excelsum		kawakawa
Melicope simplex		
Melicytus ramiflorus	whiteywood	mahoe

Table A1.1 Species list for the ten study sites.

The following species list is by no means comprehensive but outlines the most predominant species in and around plots at the ten main study sites. D = dominant (numerically dominant species), C = common (occurs throughout site), O = occasional (a few individuals), R = rare (one or two individuals), * = hybrids present.

SPECIES	Mana.	Denn	Okuti	Nikau	Blue	Puhi	Payne	Coke	Price	Perak
Gymno.										
Dac dac	R	D	O	O	C			O	O	O
Dac cup	O			O	O	O				
Pod hal				C*						C*
Pod tot	D*	D	D	D*	D	D	D	D	O	O*
Pru fer	O			O	O	O				
Pru tax		C	C	O	D	D	R	C	D	C
Angio.										
Ale exc					O	O	O		C	
Ari ser	O	O		O						
Asc luc	O									
Car ser	C	O			O					
Cop are	C				C	C	O	C	C	
Cop gra	C		O		C					
Cop rot	C				O					
Dod vis				C			O			
Ela den	O				C			O		
Ela hoo		O	O							
Fuc exc	R	C				O			O	O
Gri lit		C	O				O			
Gri luc	C							C		C
Hed arb	C		C	O	C	C	O	C	O	O
Hoh ang		O	O							
Kni exc			C			O	O			
Kun eri	R									
Mac exc			C			C	D	C	C	
Mel sim									C	
Mel ram	C	O	C	C	C	C	C	C	C	C

BOTANICAL NAME	COMMON NAME	MAORI NAME
Metrosideros robusta	northern rata	
Metrosideros umbellata	southern rata	
Myrsine australis		mapou
Paratrophis microphylla	milk tree	turepo
Pennantia corymbosa		kaikomako
Pittosporum euginoides	lemonwood	tarata
Plagianthus regius	ribbonwood	
Pseudopanax arboreus	five finger	
Pseudopanax colensoi	three finger	orihou
Pseudopanax crassifolius	lancewood	horoeka
Pseudopanax ferox		
Quintinia acutifolia	Westland quintinia	
Ripogonum scandens	supplejack	
Rubus parviflora	lawyer vine	
Schefflera digitata		pate
Sophora tetraptera		kowhai
Urtica ferox	tree nettle	ongaonga
Weinmannia racemosa		kamahi
MONOCOTYLEDONS		
Astelia solandri	lily	
Earina autumnalis	autumn orchid	
Rhopalostylis sapida		nikau
Uncinia uncinata	hook grass	
FERNS		
Asplenium bulbiferum	Hen & chickens fern	manamana
Asplenium flacidum	hanging spleenwort	makawe o raukatauri
Asplenium polyodon	sickle spleenwort	petako
Cyathea dealbata	silver tree fern	ponga
Cyathea medullaris	black tree fern	mamaku
Cyathea smithii	soft tree fern	katote
Dicksonia squarrosa	rough tree fern	wheki
Phymatosorus diversifolius	hound's tongue	kowaowao
Polystichum vestitum	prickly shield fern	puniu
Trichomanes reniforme	kidney fern	raurenga

SPECIES	Mana.	Denn	Okuti	Nikau	Blue	Puhi	Payne	Coke	Price	Perak
Met rob				R				R		
Met umb	R									
Myr aus				C	C	C		O	C	C
Par mic		R						O	C	
Pen cor			O						C	
Pit eug		C	O	C		O		O	O	C
Pla reg		C								
Pse arb		O	O			C				
Pse col	R	O								
Pse cra	C	O	O	O			O	O		O
Pse fer								O		
Qui acu	O									
Rip sca	C	C	C	O	C	C	O	C	C	C
Rub par	O			O					C	C
Sch dig	C	C					O			C
Sop tet			O	C				C		
Urt fer		R			O				C	
Wei rac	D	C		O		O				
Mono.										
Ast sol	C	O		O			O			
Ear aut	C			O						
Rho sap				C			O	O		
Unc unc	C	C		O	C					
Ferns										
Asp bul	C	O	O		O	C	C		C	C
Asp fla	C	C		O	C	C		C		C
Asp pol	O			C			C			
Cya dea					O			O		C
Cya med								O		
Cya smi	C									
Dic squ	C									
Phy div	C	C		C						
Pol ves		C								
Tri ren	C			O						

Table A1.2 Voucher herbarium specimens deposited in the University of Canterbury Herbarium (CANU).

SPECIES	LOCALITY	Voucher No.
Alectryon excelsus	Prices Valley, Banks Peninsula	37217
Aristotelia serrata	Peel Forest, Canterbury	37215
Asplenium bulbiferum	Paynes Ford S.R., Golden Bay	37220
Asplenium polyodon	Paynes Ford S.R., Golden Bay	37221
Clematis vitalba	Peel Forest, Canterbury	37211
Dac. dacrydioides (female)	Prices Valley, Banks Peninsula	37201
Dac. dacrydioides (seedling)	Prices Valley, Banks Peninsula	37199
Dacrycarpus dacrydioides	Peel Forest, Canterbury	37202
Dacrycarpus dacrydioides (mle)	Prices Valley, Banks Peninsula	37200
Earina autumnalis	Nikau S.R., Punakaiki	37210
Fuchsia excorticata	Peel Forest, Canterbury	37214
Melicope simplex	Prices Valley, Banks Peninsula	37216
Melicytus lanceolatus	Peel Forest, Canterbury	37203
Myrsine australis	Nikau S.R., Punakaiki	37208
P.totara x acut. aff. waiho (sedlg)	Mananui Bush S.R., Westland	37181
P.totara x acut. aff. waihoensis	Mananui Bush S.R., Westland	37180
P.totara x hallii	Nikau S.R., Punakaiki	37179
Pittosporum euginoides	Peel Forest, Canterbury	37212
Plagianthus regius	Peel Forest, Canterbury	37209
Podocarpus acutifolius (female)	Lake Brunner, Westland	37176
Podocarpus acutifolius (male)	Lake Brunner, Westland	37177
Podocarpus hallii	Nikau S.R., Punakaiki	37174
Podocarpus hallii	Peraki Saddle, Banks Peninsula	37185
Podocarpus hallii	Peraki Saddle, Banks Peninsula	37186
Podocarpus totara	Akaroa, Banks Peninsula	37173
Podocarpus totara	Blue Duck S.R., Kaikoura	37168
Podocarpus totara	Nikau S.R., Punakaiki	37172
Podocarpus totara	Paynes Ford S.R., Golden Bay	37178
Podocarpus totara	Peel Forest, Canterbury	37167
Podocarpus totara	Peel Forest, Canterbury	37175
Podocarpus totara	Prices Valley, Banks Peninsula	37183

SPECIES	LOCALITY	Voucher No.
Podocarpus totara	Puhi Puhi S.R., Kaikoura	37182
Podocarpus totara (male)	Okuti Valley, Banks Peninsula	37170
Podocarpus totara (seedling)	Okuti Valley, Banks Peninsula	37169
Podocarpus totara (seedling)	Paynes Ford S.R., Golden Bay	37171
Podocarpus totara (seedling)	Prices Valley, Banks Peninsula	37184
Prumnopitys ferruginea	Nikau S.R., Punakaiki	37189
Prumnopitys taxifolia	Aorere River, Golden Bay	37194
Prumnopitys taxifolia	Blue Duck S.R., Kaikoura	37195
Prumnopitys taxifolia	Okuti Valley, Banks Peninsula	37196
Prumnopitys taxifolia	Paynes Ford S.R., Golden Bay	37190
Prumnopitys taxifolia	Peel Forest, Canterbury	37193
Prumnopitys taxifolia	Prices Valley, Banks Peninsula	37197
Prumnopitys taxifolia	Prices Valley, Banks Peninsula	37198
Prumnopitys taxifolia (seedling)	Prices Valley, Banks Peninsula	37187
Prumnoptiys taxifolia	Puhi Puhi S.R., Kaikoura	37191
Prunmopitys ferruginea	Blue Duck S.R., Kaikoura	37188
Pseudopanax colensoi	Peel Forest, Canterbury	37213
Schefflera digitata	Paynes ford S.R., Golden bay	37205
Schefflera digitata	Peel Forest, Canterbury	37204
Sophora microphylla	Nikau S.R., Punakaiki	37207
Sticta latifrons	Mananui Bush S.R., Westland	37218
Sticta latifrons	Nikau S.R., Punakaiki	37219
Urtica ferox	Blue Duck S.R., Kaikoura	37206

APPENDIX TWO
GEOLOGICAL MAP REFERENCES

Table A2 Geological map sheet references for the ten study sites.

STUDY SITE	Soil Map[1] 1:253440	Geol. Map[2] 1:63360	Geol. Map[3] 1:250000	NZLRI Map[4] 1:63360
Mananui S.R.	5		17	50
Nikau S.R.	3	S37		37
Dennistoun Bush	8		20	91
Okuti Valley S.R.	9		21	94
Peraki Saddle S.R.	9		21	94
Puhi Puhi S.R.	4			49
Blue Duck S.R.	4			49
Coke Covenant	1	S3		3
Payne's Ford S.R.	1	S8		3
Price's Valley Cov.	9		21	94

[1]D.S.I.R. (1965). 'General survey of soils of the South Island.' Soil Bureau Bulletin 27. 1:253440. Government Printer, Wellington.

[2]New Zealand Geological Survey (various). 'New Zealand geological survey map. 1:63360.' D.S.I.R., New Zealand.

1971 Farewell-Collingwood
1971 Takaka
1988 Punakaiki

[3]New Zealand Geological Survey (various). 'New Zealand geological survey map. 1:250000.' D.S.I.R., New Zealand.

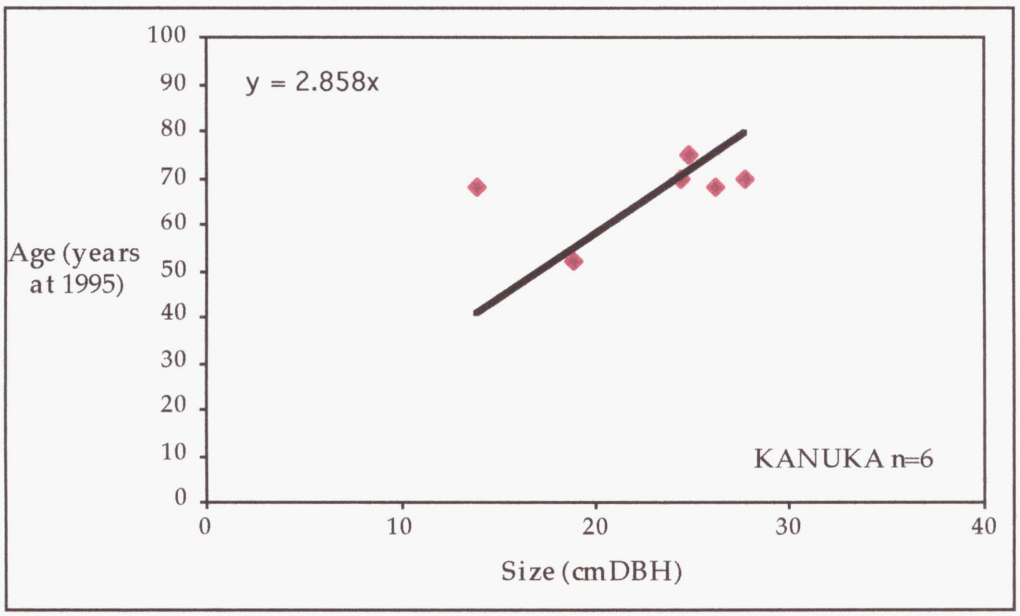
1967 Hokitika
1973 Christchurch
1975 Mt Cook

[4]Ministry of Works and Development (various). 'New Zealand Land Resource Inventory Worksheet.' 1:63360. Water and Soil Division, New Zealand.

1975 Mt Peel
1975 Akaroa
1976 Hokitika
1978 Clarence
1978 Collingwood-Farewell
1978 Kaikoura
1978 Punakaiki
1978 Takaka

APPENDIX THREE
KANUKA SIZE VERSUS AGE REGRESSION

Figure A3 Size versus age regression for kanuka cross sections.



APPENDIX FOUR
PUBLIC QUESTIONNAIRE

Details of all public correspondence appear below in chronological order.

April 1996 - Covering letter and draft questionnaires written.
3rd April 1996 - Finalised questionnaires delivered to 125 households in Okuti Valley and Little River areas after receiving telephone confirmation of Human Ethics Committee approval.
16th April 1996 - Official Human Ethics Committee approval received.
August 1996 - Final compilation of results. Reply letter and summary of results sent to people who requested further information.
December 1996 - Summary of results sent to people who requested further information.
Upon completion (31st March 1998) - Notice of summary report deposit in Little River Library.

Table A4.1 Tally of questionnaire return times and number of respondents requesting further information.

Return time (weeks)	N returned	N request information
1	20	10
2	25	16
3.5	10	4
5	3	-
7	2	2
9	2	1
15	2	1
TOTAL	**64 (51.2%)**	**34 (27.2%)**

School of Forestry
University of Canterbury Private Bag 4800
Christchurch New Zealand
Telephone: 03-364 2117
Fax: 03-364 2124

3rd April 1996

The Resident(s)
Little River and Okuti Valley area
BANKS PENINSULA

Dear sir/madam

Hello. My name is Rachel Ebbett and I am conducting PhD research at the University of Canterbury into the ecology of lowland totara, which was once a common tree on the Peninsula. My supervisor is Dr David Norton in the School of Forestry. Part of my study involves the preparation of an integrated landscape management plan to provide for the survival of totara in the future and the protection of soil and waterways.

You are invited to participate in this project to determine public attitude to land management and trees in the landscape by completing the following questionnaire. I would like one member of the household to fill out the short questionnaire and return to me in the enclosed stamped addressed envelope, hopefully by the end of April. Information will be analysed and reported on in my thesis and possibly in publications arising from my research.

By completing the questionnaire it will be understood that you consent to publication of the results with the understanding that you will remain anonymous. This questionnaire has been reviewed by the University of Canterbury Human Ethics Committee.

I will be pleased to discuss any concerns you may have about participation in the project and I can be contacted at home on (03)3749083. I have included a section which you can fill in if you wish to view the results of this study at the end of the year. Thank you for your time.

Yours sincerely

R.L.Ebbett

QUESTIONNAIRE
LAND MANAGEMENT AND TREES IN THE LANDSCAPE
Little River and Okuti Valley residents

First I would like to ask some questions about the area you live in.

1. How long have you resided in the Okuti Valley/Little River area?_____months/years

2. How large is the land you occupy?_____acres/hectares

3. What is produced on the land you occupy? Tick as many as apply.

Nothing	[ ]
Stock animals/wool	[ ]
Garden crops	[ ]
Agricultural crops	[ ]
Orchard fruit/nuts	[ ]
Timber	[ ]
Bees/honey	[ ]
Other_____	

4. Why do you live in this area? Tick as many as apply.

Nice place to live	[ ]
Good community	[ ]
Close to Christchurch	[ ]
Family reasons	[ ]
Good climate	[ ]
No particular reason	[ ]

Other reasons?_____

_____

5. Are you involved with any of the following in this area?

Sports teams or clubs	[ ]
Social clubs	[ ]
School activities/committees	[ ]
Conservation groups	[ ]
Lions Club, Rotary Club, Kiwanis	[ ]
Senior citizen groups	[ ]
Volunteer work	[ ]
Planning groups/committees	[ ]

Are you involved in any other community groups not mentioned above?

_____

_____

6. Have you visited the Department of Conservation Scenic Reserve in Okuti Valley Road (Okuti Valley Scenic Reserve)?

DON'T KNOW [ ]	
YES [ ]	
NO [ ]	go to Q9

7. How often did you visit this reserve in the last year? Tick which best applies.

Once	[ ]
A few times	[ ]
Once a month or more	[ ]

8. Okuti Valley Scenic Reserve is a totara/matai forest with an area of regenerating totara and matai under kanuka. What do you like about the reserve? Tick as many as you like.

Nothing	[ ]
Good example of totara/matai forest	[ ]
Birdlife	[ ]
Place to walk	[ ]

Other_____

_____

9. Have you visited Birdlands Native Park Trust in Okuti Valley?

DON'T KNOW [ ]
YES [ ]
NO [ ]

If yes, how often did you visit in the last year? Tick which best applies.

Once	[ ]
A few times	[ ]
Once a month or more	[ ]

10a. I would like you to think about the Little River and Okuti Valley catchment areas. What do you think of the amount of exotic plantations? (eg. orchards, pines etc.)

[ ] [ ] [ ] [ ] [ ]
Not enough About right Too much

Comments_____
_____

10b. What do you think about the amount of native forest? (including kanuka)

[ ] [ ] [ ] [ ] [ ]
Not enough About right Too much

Comments_____
_____

11. In general, what do you consider to be the benefits of planted trees? Tick as many as you like.

	EXOTIC	NATIVE
No benefits	[ ]	[ ]
Income	[ ]	[ ]
Human food	[ ]	[ ]
Aesthetic properties	[ ]	[ ]
Bird habitat and food	[ ]	[ ]
Privacy	[ ]	[ ]
Timber	[ ]	[ ]
Wind shelter	[ ]	[ ]
Stock fodder	[ ]	[ ]
Erosion control	[ ]	[ ]
Waterway protection	[ ]	[ ]
Forest regeneration	[ ]	[ ]

Other_____

I would now like to ask a few questions about land management.

12. If the finances were available, which of the following (if any) land uses would you consider?

Farming stock	[ ]
Agricultural crops	[ ]
Orchard crops	[ ]
Timber crops	[ ]
Bees/honey production	[ ]
Shelter belts	[ ]
Fodder crops for stock	[ ]
Erosion control planting	[ ]
Waterway protection planting	[ ]
Native forest regeneration	[ ]
None	[ ]

Others_____

_____

13. Who do you think should provide funding for the planting of erosion control trees on private land in the Little River and Okuti Valley areas?

No-one	[ ]
Land owners	[ ]
Community groups	[ ]
Local council	[ ]
Regional council	[ ]
National government	[ ]
Other	[ ]

Comments_____

_____

14. Who do you think should provide funding for the regeneration of native forest on private land in the Little River and Okuti Valley areas?

No-one	[ ]
Land owners	[ ]
Community groups	[ ]
Local council	[ ]
Regional council	[ ]
National government	[ ]
Other	[ ]

Comments_____

_____

15. Do you think an integrated landscape management approach on the catchment level (combining erosion control, aesthetic planting's, diverse land use etc.) would be of benefit...

to you?	YES [ ]	NO [ ]
to the community?	YES [ ]	NO [ ]

16. Do the land management practices of your neighbours affect you? (eg. spraying, planting, water use etc.)

YES [ ] NO [ ]

If yes, in what ways?

_____

_____

PERSONAL INFORMATION Please only fill out those questions you feel comfortable answering.

Where you are resident, do you...

own (including mortgage) YES [ ] NO [ ]

rent or lease YES [ ] NO [ ]

Other_____

SEX female [ ] male [ ]

AGE (years)

0 - 20 [ ]
21 - 35 [ ]
36 - 50 [ ]
51 - 70 [ ]
70 - on [ ]

ANNUAL INCOME ($)

0 - 9,999 [ ]
10,000 - 19,999 [ ]
20,000 - 29,999 [ ]
30,000 - 39,999 [ ]
40,000 - 49,999 [ ]
50,000 - 59,999 [ ]
60,000 - or more [ ]

Thanks very much for taking the time to answer this questionnaire. If you would like to view the results of my study, please write your name and/or address below.

Name_____

Address_____

_____

(This section on separate sheet as per Ethics Committee recommendation).

School of Forestry
University of Canterbury Private Bag 4800
Christchurch New Zealand
Telephone: 03-364 2117
Fax: 03-364 2124

16 April 1996

Ms R Ebbett
C/- Dr D Norton
School of Forestry
UNIVERSITY OF CANTERBURY

Dear Ms Ebbett

The Human Ethics Committee has considered and approved your research proposal **"Land Management and Trees in the Landscape - Questionnaire"**. However, the Committee draws your attention to the need to have names and addresses on a sheet separate from the questionnaire.

The Committee also returns three spare copies of your application.

Yours sincerely

J A Cockle (Miss)
Secretary

School of Forestry
University of Canterbury Private Bag 4800
Christchurch New Zealand
Telephone: 03-364 2117
Fax: 03-364 2124

August 1996

The Residents
Little River and Okuti Valley areas
BANKS PENINSULA

Dear_____

Thank you for taking the time to complete my questionnaire and return it. I have enclosed results which outline the responses received. Questionnaires were delivered to practically every house in the area (approximately 125) and 64 were returned completed.

Responses show that residents of your area are keen on the protection of bird habitat, waterways, and native forest. Many people said they would be willing to plant natives on their property, particularly for erosion control which is a major problem on the Peninsula. The majority of respondents thought an integrated land management approach would be of benefit to themselves and the community, with funding for erosion control plantings and native forest regeneration being provided by both land owners and Regional Council.

As part of my PhD thesis I am now developing an integrated land management plan for the Okuti Valley catchment which will provide for diverse economic land-use as well as landscape enhancement by way of protection plantings. Avenues will be explored in terms of land owner options and funding sources. This plan is theoretical only and it will be up to individual land owners to decide if there is anything of value in it for them and their community. Okuti Valley was chosen as an example catchment but integrated land management can be adopted anywhere using the same guidelines.

When my thesis is completed I will deposit a copy in the Little River library and let you know. Thanks again for your interest and don't hesitate to contact me if you wish to discuss anything.

Yours sincerely

R.L.Ebbett

School of Forestry
University of Canterbury Private Bag 4800
Christchurch New Zealand
Telephone: 03-364 2117
Fax: 03-364 2124

31st March 1998

Residents of Okuti Valley
and Little River, Banks Peninsula.

Dear Resident,

Thanks for your response to my questionnaire concerning land management and trees in the landscape. I have now completed my PhD and a summary report of my thesis has been deposited at the Little River library. Please feel free to go and check it out. I'm sure you will find the results interesting.

The integrated landscape plan presented in Chapter Twelve was mainly an academic exercise to investigate whether this type of approach could be of use for providing for the future survival of lowland totara while allowing for existing land uses. This plan was theoretical only and any land management plans to be implemented would only proceed after discussions with landowners. The design principles are based on the Banks Peninsula Proposed District Plan (1997). Only Okuti Valley was used in the formulation of the integrated land management plan. The reason for this was logistical, only one catchment could be used and Okuti Valley was the most suitable. However, the principles used in Chapter Twelve of my thesis can readily be applied to the entire Peninsula.

The results of the questionnaire and resultant integrated land management plan were presented at an international conference in Taupo in December 1997 and received with interest. All respondees remained confidential. Once again thanks for your time. Good luck with your future land management and tree planting.

Yours sincerely

R.L.Ebbett

APPENDIX FIVE
PUBLICATION DETAILS

Publications arising from the current research;

Ebbett,R.L. (in prep.). 'Integrated landscape management - a case study using a fragmented forest species.' Contents of Chapter Eight and Nine. Presented at 'Nature Conservation in Production Environments' conference, Taupo, December 1997, and submitted for publication in proceedings of the conference (Nature Conservation 5). All literature review, questionnaire results, data analysis, and 1st draft writing by R.L.Ebbett. Status: Final draft stage, submitted 2nd December 1997.

Ebbett,R.L.; Norton,D.A. (in prep). 'The ecology of endemic Podocarpus: a review.' Represents all literature reviewed in present study, particularly Chapter Two. All literature review research and data analysis, and 1st draft writing by R.L.Ebbett, 2nd draft editing by D.Norton. Status: in preparation, final draft stage.

Ebbett,R.L.; Hall,R. (in prep.). 'A disturbance mediated lowland podocarp forest.' Represents section 4.3. 1st draft writing and all data analysis by R.L.Ebbett, 2nd draft and geology section by R.Hall. Data is from both authors. Status: in preparation, 2nd draft stage.

Publications arising from previous research;

Ebbett,R.L.; Ogden,J. (1998). 'Seedling growth of five endemic New Zealand podocarp species under different light regimes.' *New Zealand Journal of Botany* 36 (2). Results of MSc study (Ebbett 1992) used in present discussion of podocarp regeneration strategies. All experimental work, data analysis, and 1st draft writing by R.L.Ebbett, 2nd draft editing by J.Ogden. Status: Accepted for publication 31st October 1997.